

SYSTEMATICS OF THE  
LAND AND FRESH-WATER MOLLUSCA  
OF THE NEW HEBRIDES

ALAN SOLEM

*Curator, Division of Lower Invertebrates*

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# Systematics of the Land and Fresh-Water Mollusca of the New Hebrides<sup>1</sup>

## INTRODUCTION

This study summarizes our present knowledge of the New Hebridean land and fresh-water Mollusca and surveys the distribution patterns of Pacific land snails. Too little collecting has been done in the New Hebrides to allow much discussion of speciation. It is only possible to discuss the nomenclatural status of the named forms, summarize the limited distributional data, and suggest possibilities for field studies. More attention has been focused on trying to determine the relationship of the New Hebridean species to those found on other islands of the Pacific. Resulting from these comparative studies are the tentative phylogenetic trees of the land Mollusca (figs. 10 and 11) and the discussion of Indo-Pacific land snail geography (pp. 245-331).

The major impetus to this study was provided by the collections made on Florida Island in the Solomons, and on Espiritu Santo in the New Hebrides, by Robert E. Kuntz from 1943 to 1945, and presented to the University of Michigan Museum of Zoology in 1947. Check-lists of the New Hebridean marine mollusks and a study on the Florida Island land and fresh-water species are in press.

Attempts to identify the Espiritu Santo land and fresh-water snails soon involved summarization of the New Hebridean fauna, based on material in American museums. The few species known from the Santa Cruz Islands (see Appendix II) are considered here, since their affinities are with New Hebridean, not Fijian or Solomon Island taxa.

The only previous comprehensive study of the New Hebridean non-marine mollusks is a checklist (Kobelt, 1881, pp. 19-20) compiled solely from descriptive literature. Of the fifty-four species listed, five are synonyms, eleven are from Lord Howe Island off

<sup>1</sup> Modified from a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the University of Michigan, 1956.

Australia, and eleven are from other localities not in the New Hebrides. Only twenty-seven represent valid records. Sykes (1903) reported thirty species from various New Hebridean localities and recorded sixteen estuarine mollusks. The other literature specifically concerned with New Hebridean non-marine mollusks is the scattered pre-1870 descriptions by Louis Pfeiffer in the Proceedings of the Zoological Society of London and short papers by Cox (1870), E. A. Smith (1884), Thomson (1885), Hartman (1886, 1888, 1889, 1890, 1891), Ancey (1896, 1897, 1905, 1906), Mabille (1895), Grimpe and Hoffmann (1925a), and Hoffmann (1929b). All of these papers are purely descriptive in character and are based on incidental collections. Except for a few species found by John Brazier in 1865 and described by Cox (1870), no New Hebridean material has been collected by a malacologist or even a person primarily interested in mollusks. The specimens in museums were either a by-product of expeditions oriented toward the collecting of other phyla or were haphazard gatherings by missionaries, traders, or planters untrained in science. It is remarkable, and extremely unfortunate, that prior to 1955 no person working on the mollusks of the Bismarcks, Solomons, and New Hebrides had ever been to the islands, much less collected the material on which his publications were based. It is hoped that my own lack of field experience in the area can be remedied in the near future.

The age of the literature pertaining to the New Hebrides only reflects the general status of land snail taxonomy during the twentieth century. In the latter part of the nineteenth century, several devoted collectors visited the Pacific islands and many papers were written on their findings. W. Harper Pease, Andrew Garrett, Eduard Graeffe, J. Kubary, Otto von Moellendorff, Xavier Montrouzier, Saint-Martin Souverbie, John Brazier, and Edgar Leopold Layard laid the foundations of our knowledge. The papers of Pease, Garrett, and Moellendorff were based on material that they had collected, while the field efforts of the others resulted in the many papers of Mousson, Gassies, Hartman, Crosse, Ancey, and Fischer.

During the twentieth century the only important land snail collectors in the Pacific have been the late C. Montague Cooke and his protégé, Yoshio Kondo, both of the Bernice P. Bishop Museum, Honolulu. Cooke published comparatively little, but his collections are invaluable and it will be many years before they have been fully studied.



In the last fifty years the important publications on Pacific snails have been few in number. Excellent monographs of the Partulidae (Pilsbry, 1909), Tornatellinidae (Pilsbry and Cooke, 1915-16), and Limacacea (H. B. Baker, 1938b, 1940, 1941) overshadow lesser ones of the Athoracophoridae (Grimpe and Hoffmann, 1925a) and Helicinidae (Wagner, 1907-11). Faunal studies on Australia (Hedley and Iredale), New Zealand (Suter, Powell, and Dell), New Caledonia (Dautzenberg and Franc), Hawaii (Pilsbry and Cooke), and Indonesia (van Benthem Jutting, Bernhard Rensch) are comprehensive, but little has been published on the fauna of the "oceanic" islands. Checklists for the Solomons (Clapp, 1923) and Hawaii (Caum, 1928); monographs of some of the endemic Hawaiian families by Pilsbry and Cooke; shorter papers by Ilse Rensch, Clench, Kondo, Abbott, Thiele, and Hoffmann; and the variational studies of Crampton and Welch, all provide fragmentary data. The phylogeny and zoogeography of Pacific land snails were discussed by Hedley (1892a, 1899), Pilsbry (1900b, 1916, 1921), C. M. Cooke (1926), Germain (1932, 1934), and H. B. Baker (1941). All these studies were based on the Polynesian fauna and their conclusions are greatly altered when the Austro-Melanesian fauna is considered as a unit.

The brief survey of the literature given above shows that, except for the Limacacea (see H. B. Baker, 1938b, 1940, 1941), the study of Pacific land snails has not benefited from the use of the "New Systematics." The many older publications contain a wealth of factual data waiting for synthesis and interpretation in the light of modern systematic theory. In trying to determine the relationships of the New Hebridean species, I found it necessary to review the classification of a number of families. Since this was primarily a faunal survey, it was not possible to revise thoroughly any family or any widely distributed genus. In most cases the available data suggested probable phylogenetic sequences and distributional patterns, but the information needed to test the hypothetical solutions was not available. Study of the shells and the few references in the literature to the anatomy of the Pacific Succineidae, Endodontidae, Bulimulidae, and Paryphantidae resulted in new interpretations of distribution, generic units and phylogeny, which, if confirmed by subsequent research, will greatly change widely held concepts of the age, origin, and means of dispersal of the land snails. The systematic review (pp. 29-204) thus contains data bearing on the classification of snails from all parts of the Pacific as well as the New Hebrides.

I have recognized 79 species as occurring in the New Hebrides and Santa Cruz Islands, although several additional names are listed in the systematic review. In several cases the material needed to prove the specific identity of named morphological variants was not available. These "species" are retained as nomenclatural units, but their probable relationship to other species is clearly indicated in the text and they are not accepted as valid species records. Sixteen new species and subspecies (listed on p. 331) and six new supra-specific names (listed on p. 332) are proposed.

The major portion of this study was done at the University of Michigan Museum of Zoology from June, 1954, through May, 1956. Revision of the systematic review and expansion of the zoogeographical survey was completed at Chicago Natural History Museum in the following year.

In preparing this report, I have been aided by many people. For permission to study collections under their charge and for loan of specimens I am indebted to Drs. Fritz Haas (Chicago Natural History Museum), the late Henry A. Pilsbry and R. Tucker Abbott (Academy of Natural Sciences of Philadelphia), Harald A. Rehder (United States National Museum), William J. Clench (Museum of Comparative Zoology), and Juan José Parodiz (Carnegie Museum, Pittsburgh), Commander Walter B. Miller (Falls Church, Virginia), and Messrs. W. K. Dell (Dominion Museum, Wellington, New Zealand) and William D. Clarke (American Museum of Natural History). Drs. Lothar Forcart (Musée d'Histoire Naturelle de Bâle), André Franc (Muséum d'Histoire Naturelle, Paris), the late Guy L. Wilkins (British Museum [Natural History]), Yoshio Kondo (Bernice P. Bishop Museum, Honolulu), and Donald F. McMichael (Australian Museum, Sydney) sent photographs and information about specimens I was unable to see personally. Data on specific taxa were generously provided by Drs. William J. Clench, Joseph P. E. Morrison, Yoshio Kondo, R. Tucker Abbott, and Henry van der Schalie. Dr. Juan José Parodiz made available notes on South American non-marine fossil mollusks; Dr. Harry S. Ladd provided data on Pacific geology and the fossil organisms found at Bikini Atoll. The late Emmett Reid Dunn read the section of general systematics; and Drs. Yoshio Kondo, Theodor Just, and the late Karl P. Schmidt read the section on zoogeography.

For help with the preparation of the manuscript I am indebted to Mr. Dwight L. Chapman, Mr. William L. Cristanelli (pls. 1 and 2), Mr. Harold J. Walter, Mrs. Phyllis Kanno, the late J. Speed

Rogers, and the members of my doctoral committee at the University of Michigan. The revision of the manuscript has been aided by my colleagues at Chicago Natural History Museum, particularly Dr. Fritz Haas and the late Karl P. Schmidt. They first interested me in zoology and through the years have devoted many hours of their time to furthering my biological career. Their help in the preparation of this paper has been invaluable. The beautiful illustrations of minute species (pls. 29-34) are the work of E. John Piffner and most of the text figures were rendered by Marian Pahl, both of Chicago Natural History Museum, Division of Illustration.

In particular I am indebted to Dr. Henry van der Schalie of the University of Michigan. His constant encouragement, constructive criticisms, and generous support have made possible what at times seemed an impossible task. Without the help he has given me this study would never have been finished.

### Historical Notes

Many explorers visited the New Hebrides between 1595 and 1825 (see Markham, 1873; Bourge, 1906; and Harrisson, 1937), but there are no records of the collecting of mollusks until the voyage of the *Astrolabe* to Vanikoro and Ticopia in the Santa Cruz Islands in 1828 (see Quoy and Gaimard, 1832-35). The many marine shells and four species of land snails—*Partula vanikorensis*, *Pleuropoma taeniata*, *Trochomorpha* sp., and an unidentifiable *Truncatella*—represent the largest collection made until less than twenty years ago. Some of the specimens are still preserved in the Muséum d'Histoire Naturelle, Paris.

In the late 1820's sandalwood was discovered in the islands and the ships of the China trade visited the southern New Hebrides regularly. George Bennett was at Dillon's Bay, Erromanga, on August 24, 1829, and collected the first living specimen of *Nautilus pompilius* (Linnaeus) seen by a European. After the trading voyage was over, the specimen was sent to London and formed the basis of the classic memoir on the "pearly nautilus" by Richard Owen (1832).

No information on collectors in the 1840's and early 1850's was available to me. During this period missionaries were attempting to settle on the islands and a few of the larger land snails of Aneiteum, Tanna, and Erromanga reached London and were described by Louis Pfeiffer between 1852 and 1861. Some came from a missionary, Rev. Turner, and a specimen of *Placostylus* collected by the famous Nova Scotian missionary, John Geddie, is still preserved

(USNM 23017). The bloody history of the settlement of the New Hebrides is well known. Several times gunboats were sent from New Caledonia to raid native villages in retaliation for the deaths of traders and missionaries, and the cruises of the *Herald* in 1854, with John MacGillivray as naturalist, and the *Curaçao* in 1865, with John Brazier of Sydney, resulted in small shell collections. MacGillivray revisited the southern New Hebrides in 1858, 1859, and 1860 (Iredale, 1937c, p. 60), but Brazier only made the one trip, touching briefly at Aneiteum, Tanna, Erromanga (where he collected shells while under attack by the natives!), Vate, and Vanua Lava (see Brenchley, 1873). Brazier found several minute species (Cox, 1870) as well as large, showy shells.

In the 1850's the expanding sugar-cane plantations of Fiji and Queensland caused an acute labor shortage and New Hebridean natives were impressed as indentured field hands. The boat trips between the New Hebrides and Queensland probably resulted in some chance introductions. *Aneitea brisbanensis* W. Pfeiffer (1900) may have been carried to the botanical gardens of Brisbane on plants from the New Hebrides. Since plants were carried as food on the voyages, *Triboniophorus graeffei* Humbert, a Queensland species, could have been carried to the New Hebrides if the locality record of Glamann (1903) is correct. *Rhachistia histrio* (Pfeiffer) is an arboreal snail found in New Caledonia, Vate, Tanna, and Queensland. The order of introduction is unknown, but I suspect a New Caledonia–New Hebrides–Queensland sequence. The original home of *R. histrio* may be Madagascar.

In the 1870's and 1880's many plantations were established in the New Hebrides. Edgar Leopold Layard, the British Consul at Noumea, New Caledonia, was an ardent shell collector and exploited the potentialities of his position. Layard sent old European newspapers to New Hebridean planters in exchange for shells found by the planters while clearing land. George de Lautour on Espiritu Santo and W. Glisson on Vate are the only ones whose names were recorded, but there were undoubtedly others. Layard sent specimens to C. F. Ancey in France, who described several species between 1884 and 1906, and to William D. Hartman in Philadelphia, who published papers between 1886 and 1891.

Most of Hartman's types and the correspondence from Layard are preserved at the Carnegie Museum, Pittsburgh, and were made available by Dr. Juan José Parodiz. Prior to Layard's fatal illness, he and Hartman planned to summarize the New Hebridean land

snail fauna. Numerous preliminary notes in the Layard correspondence have been incorporated into this study. Layard's collection was purchased by the late E. R. Sykes and is now in the British Museum (Natural History).

Material collected primarily (if not entirely) on Espiritu Santo by Dr. Ph. François was studied by Jules Mabille (1895). Mabille's identifications were inaccurate and all his unconfirmed records have been rejected as unreliable (see Ancey, 1905). Dr. André Franc kindly provided photographs of the types of several of Mabille's unfigured species in the Paris Museum (see pl. 12). J. J. Walker, a ship's engineer, collected specimens during the cruise of the *Ringarooma* between June and October, 1900 (see Sykes, 1903), and found three new species. Felix Speiser, an anthropologist, who was working on Malo and Espiritu Santo in 1911 (see Grimpe and Hoffmann, 1925a), found slugs which are now in Basel, Switzerland. Dr. Lothar Forcart was unable to locate any other mollusks collected by Speiser. Professor John R. Baker of Oxford visited Espiritu Santo and Gaua in 1922 and 1927 and spent a year (1933-34) at Hog Harbour, Espiritu Santo. He made general biological collections and the mollusks were turned over to Guy Robson of the British Museum (Natural History). The slugs were studied by Hoffmann (1929b) and a few notes on the fresh-water snails were published by J. R. Baker (1929). The material in the British Museum was not located until 1958 and reached me while this monograph was in press. A detailed report will be issued later, but a few important notes have been added below.

E. Aubert de la Rue was in the New Hebrides from 1934 to 1936. The marine shells (Fischer and Fischer-Piette, 1938, 1939) and the fossils he collected (Abrard, 1946) are in the Paris Museum. I was unable to determine if he collected any non-marine shells. L. Macmillan, of the Whitney South Sea Expedition, picked up a few shells on Tanna, Aneiteum, and Erromanga, in 1937. They were deposited in the American Museum of Natural History and lent to me for study. Several members of the United States Armed Forces made collections during World War II. Those that could be located are mentioned below. Undoubtedly many more are still in private hands.

### Material Studied

About 5,100 specimens (581 lots) of New Hebridean land and fresh-water shells were examined. The largest single collection, 225

lots, was made by Robert E. Kuntz on southeastern Espiritu Santo (see pl. 2 and Appendix I). Kuntz not only established geographic collecting stations but often divided each site into ecologic niches. My observations on the status of *Trochomorpha rubens* vs. *T. convexa*, *Pleuropoma albescens* vs. *P. sublaevigata*, *Dendrotrochus layardi*, and the *Diplomorpha* complex all derive directly from the Kuntz ecological notes. Of particular value in the Kuntz material were the many specimens preserved in alcohol, the shells from an alluvial deposit (ML 33), and a stream drift sample (ML 95). The Kuntz collection is now integrated into the mollusk collection of the University of Michigan Museum of Zoology, with a duplicate set in Chicago Natural History Museum and paratypes of new species distributed to several other institutions. Besides the non-marine shells, Kuntz collected 331 lots of marine and about 150 lots of estuarine Mollusca.

During the summer of 1954, six museums in the eastern United States were visited and their mollusk collections searched for New Hebridean material. The relevant specimens were borrowed and studied over the period of the next two years. The institutions visited and the number of lots from each are: Carnegie Museum, Pittsburgh (43 lots); American Museum of Natural History (29 lots); Museum of Comparative Zoology, Harvard (53 lots); Academy of Natural Sciences of Philadelphia (51 lots); United States National Museum (29 lots); and Chicago Natural History Museum (12 lots). The Bryant Walker collection at the University of Michigan added 104 lots of New Hebridean shells. Most of the lots were from famous shell collections and many were types or from the type lots. Some previously unstudied material was located, however.

Throughout the text, the following abbreviations indicate the depository of the specimens referred to:

|        |   |
|--------|---|
| AMNH   | American Museum of Natural History          |
| ANSP   | Academy of Natural Sciences of Philadelphia |
| BM     | British Museum (Natural History)            |
| BPBM   | Bernice P. Bishop Museum, Honolulu          |
| CM     | Carnegie Museum, Pittsburgh                 |
| CNHM   | Chicago Natural History Museum              |
| DMNZ   | Dominion Museum, Wellington                 |
| MCZ    | Museum of Comparative Zoology, Harvard      |
| Miller | Walter B. Miller, Falls Church, Virginia    |
| ML, NH | Kuntz station numbers (see Appendix I)      |
| UMMZ   | University of Michigan Museum of Zoology    |
| USNM   | United States National Museum               |

### Geography of the New Hebrides

The New Hebrides (pl. 1) comprise approximately eighty islands lying between 12° and 20° S. Lat. and 165° and 170° E. Long. They extend about 550 miles northwest to southeast, from the northernmost island, Hiu in the Torres Group (165° 40' E., 13° 10' S.), to the southernmost, Aneiteum (169° 51' E., 20° 15' S.). They are about 1,100 miles east of, and roughly parallel to, the coast of northern Queensland.

The Santa Cruz (Queen Charlotte) Islands lie 100 miles north of the Torres, and the main island, Santa Cruz (Ndeni, Nitendi), is about 240 miles east of San Cristoval in the Solomons; the Loyalty Islands are about 120 miles southwest of Tanna; New Caledonia is 70 miles beyond the Loyalties; the Fijis are about 400 miles east of the New Hebrides; and the southern Solomon Islands are about 300 miles northwest of the Torres.

The depth of water separating the various archipelagoes is as important as geographic proximity. Detailed information on the contour of the Pacific Ocean is difficult to find, but a few general conclusions can be drawn. Sarasin (1925, pp. 5, 6) gave charts showing the 2000-meter and 3000-meter contour lines for the Melanesian–New Zealand region. The 2000-meter contour joins the New Hebrides and Santa Cruz Islands but leaves them isolated from New Caledonia and the Solomon Islands. The 3000-meter contour connects the New Hebrides to the Solomons and New Guinea but probably not to New Caledonia. New Caledonia is joined to the Louisiades and New Guinea by a separate submarine ridge through the Huon group. The possible importance of the undersea topographic features is discussed in the section on geology and referred to frequently in the zoogeographic summary (see also Riech, 1937, pp. 138–141).

The New Hebrides thus form a natural geographic unit isolated by both distance and oceanic deeps from the neighboring archipelagoes. The islands are arranged in a "Y," the tail extending from Vate to Aneiteum, one arm through the Sheppard group north to Maewo, and the other arm through Malekula to Espiritu Santo. The small Torres and Banks groups lie north of Espiritu Santo. Information about the different islands is scattered through many books and periodicals. Good general accounts are given by Speiser (1913) and Aubert de la Rue (1945). Mawson (1905), Allen (1922), and Robson (1946) describe the individual islands; bibliographies are contained in Allen (1922, pp. 540–542) and Harrisson (1937).

The following list of the principal islands gives alternate names, prominent geographic features, and the names of people who collected shells from each. The sequence is from south to north.

Aneiteum (Anatom, Annaton, Annatom, Annatam, Aneitym) lacks the raised coral reefs characteristic of most of the other islands. Geddie, Brazier, MacGillivray, Turner, and Macmillan collected, usually near Anelgauhat Bay.

Tanna (Tana) is well wooded and mountainous, with an active volcano, Yasowa (Yasur), whose sulphurous fumes produce a central "desert." Turner, MacGillivray, J. J. Walker, Robertson, and Macmillan collected near Port Resolution and White Sands.

Aniwa (Immer, Nina) is a small coral island located 15 miles east-northeast of Tanna. Native tradition says it was formerly connected to Tanna by a land bridge (see Mawson, 1905, p. 408). Boettger (1916) lists a few mollusks collected by the Hamburg Süd-See Expedition.

Futuna (Erronan, Foutouna, Table-Top) is a volcanic island, 1,930 feet high, lying 44 miles east of Tanna. Macmillan found a few juvenile *Placostylus* there in 1937.

Erromanga (Eromanga) has an extensive savannah area and a few raised coral platforms up to 1,000 feet elevation. Dillon's Bay is the most important locality, and Turner, MacGillivray, Brazier, and Macmillan collected on the island.

Vate (Efate, Esafate, Sandwich) has mountains in the northern and western portions. No mollusks have been collected on the central and southern plain, but Havannah Harbour, Undine Bay, and Vila (Fila) have been visited by Brazier, Glisson, J. J. Walker, Froggatt, and Miller.

Nguna Island off the coast of Vate has a few marine shells reported from it.

Epi (Api, Tasiko) is mountainous and was briefly visited by the *Challenger* Expedition (see E. A. Smith, 1884).

Ambrym (Ambrim) has no known land mollusks, although slugs have been observed on the island (see Grimpe and Hoffmann, 1925a).

Pentecost (Pentecote, Whitsuntide, Aragh Aragh) is a long, narrow volcanic island with a central ridge 2,500 feet high. No land snails have been collected.

Maewo (Aurora) is similar in structure to Pentecost. Mollusks have never been collected.

Omba (Oba, Aoba, Isle of Lepers) lacks raised coral reefs. F. P. Drowne collected a few *Diplomorpha* there in 1927.

Malekula (Malicolo, Mallicolo) is less densely forested in the lowlands than is Espiritu Santo. A few shells have been picked up at Port Sandwich and the satellite islands, Vao and Rano. Bougainville Strait between Malekula and Espiritu Santo is less than 300 feet deep, and the two islands probably were connected during the Pleistocene glaciation.

Espiritu Santo (Santo, Marina) is the largest island (1,500 square miles). There are several permanent rivers (Jordan, Sarakata, Renee) and a chain of mountains which reach 5,566 feet (Santo Peak or Iaiiriri) and 6,195 feet (Mount Tabwemasana). The eastern part of the island is a coral platform elevated 300 to 600 feet. Most of the collecting has been done on the extreme southeastern portion of the island near Segond Channel, the Malo pass, and the satellite islands:



Aore (Aura), Malo (St. Bartholomew), Tutuba (Sitova), Araki, and Tangoa (see pl. 2). A few shells have been picked up at Hog Harbour, Terebiu Mission (Terebu) on St. Phillips and St. James Bay (Big Bay), and Cape Lisburn. J. R. Baker found slugs in the interior of the island (see Hoffmann, 1929b). The most important collectors were George de Lautour (1880's), Ph. François (1890's), Felix Speiser (1911), and Robert E. Kuntz (1943-44).

Gaua (Santa Maria, Lacona) has a large fresh-water lake (four miles in circumference) in the center of the island. J. R. Baker found some mollusks in this lake and J. J. Walker collected snails from other parts of the island in 1900.

Valua (Saddle, Mota-Lava) was visited by J. J. Walker in 1900. Mawson (1905, p. 424) thought that Valua, Mota, and Vanua Lava were probably once part of a single volcanic crater.

Vanua Lava is a volcanic island reaching 3,120 feet in elevation. Brazier and J. J. Walker collected there.

In the Torres group, Hiu (Hiw, North) and Lo (Loh, Saddle) are coral limestone islands with a maximum height of 1,230 feet. J. J. Walker collected on both islands. Buka-Buka (see Ancey, 1905, p. 44) could not be recognized as an alternate name for any of the Torres Islands. The island to which it refers is unknown to me.

During the voyage of the *Astrolabe*, mollusks were collected from Tucopia (Ticopia) and Vanikoro in the Santa Cruz Islands (Queen Charlotte) (see Quoy and Gaimard, 1832-35). An Australian Museum expedition may have collected subsequently on Vanikoro, but no published record of non-marine material is available. Land snails from Santa Cruz (Ndeni) Island were collected by A. F. Basset-Hull, Troughton and Livingston (see Iredale, 1927), W. M. Mann, and possibly the Rev. C. E. Fox of Malaita in the Solomons.

### Physical Factors of the Environment

Boycott (1934) considered that the local distribution of land snails was primarily determined by moisture, shelter, and the availability of lime. The extreme importance of moisture is well summarized by Graham (1957, p. 135) who stated: "No mollusc can ever be said to have become truly terrestrial in the sense that an arthropod or vertebrate has . . . they are terrestrial, as woodlice and *Peripatus* are terrestrial, by avoiding the truly terrestrial conditions and living in restricted habitats of high humidity."

Availability of lime is undoubtedly critical and the number of obligatory calcicole species is large (Boycott, 1934, pp. 9-12). Unfortunately we do not know which forms of lime are biologically available to snails. Trübsbach (1943, 1947) suggested that only *organic* lime salts, usually citrate limes, can be utilized by the animal, but his hypothesis needs confirmation.

Boycott (1934, p. 4) also believed that food, *per se*, "has no influence either by its quality or quantity on the recurrence of our

land Mollusca." Most snails feed on decaying vegetation and fungi, but some are carnivorous, and a few feed directly on living plants. The type of plant cover supplying the decaying matter is immaterial, except for the effects it has on the *physical* nature of the habitat, i.e., acidity, shelter, moisture retention, and percentage of organic matter. Lundgren (1954, pp. 472-473) and Burch (1956, 1957) correlated snail distribution with vegetation, but I suspect that *physical* rather than *biotic* factors are involved.

In analyzing snail distributions, the micro-environment is more important than the gross conditions. Little is known of the New Hebridean macro-environment and nothing of the micro-environments, but some features of the New Hebridean climate and geology correlate with land snail distribution and variation.

#### CLIMATE

The New Hebrides extend for more than 500 miles and there are considerable differences in both temperature and rainfall between the Banks and Aneiteum. Precise data are almost unavailable and only a few general comments can be offered. The micro-climates, as determined by local topography, probably dominate most "phenotypic variation," but some New Hebridean species show variations correlated with the over-all climatic conditions.

In the southern islands the climate is distinctly seasonal, with a hot, wet period from November to April and a cool, dry season from May to October. Aneiteum, Tanna, and Erromanga have a climate much like that of New Caledonia, with an annual rainfall of about fifty inches. On Vate Island the average annual temperature is about 72° F., and there is a 9.8° F. difference between the average for the coolest month and the average for the warmest.

The climate at Hog Harbour, Espiritu Santo, was studied by Baker and Harrison (1936), who concluded that it "is hot and wet from June to October, and slightly hotter and considerably wetter from November to May." Over a period of years, the annual rainfall averaged about 120 inches, the driest month (August) averaging 5.6 inches, and the wettest (January) 11.1 inches. The average annual temperature was 79.1° F., with the hottest month (January) averaging 81.1° F., and the coolest (July) 76.8° F. The western side of Espiritu Santo, in the rain shadow of Santo Peak and Mount Tabwemasana, has less rainfall and a dryer "dry" season, but no exact data are available. The Banks Islands have over 200 inches of rain a year, but no exact data could be located.

This gradient in rainfall from 50 inches annually on Aneiteum to over 200 inches annually on the Banks, with the southern islands having a true "dry season" and the northern islands a continual "wet season," is reflected in morphological gradients in the shells of several New Hebridean land snail taxa (see pp. 22-23).

In discussing the origin of the fauna, it is necessary to consider the direction of prevailing winds and currents. Both winds and currents come from Polynesia, and even the hurricanes, about two per year (see Visser, 1925), develop near Fiji and move toward the New Hebrides and New Caledonia.

#### GEOLOGY

Mawson (1905) and Abrard (1946) provide the only important sources on New Hebridean geology. The islands are a complex mixture of metamorphic, andesitic volcanic, and coralline rocks. Only surface features have been observed, sometimes from the deck of a ship, and the geologic history of the region is unknown. Mawson (1905, p. 474) suggested that the arc of the New Hebrides was formed during the Hercynian revolution (Pennsylvanian to Permian), but the earliest known fossiliferous rocks are only Early Miocene (Abrard, 1946, p. 105), probably equivalent to the Aquitanien of Europe.

The New Hebrides are west of the "Andesite Line" and are a region of great seismic activity. Volcanoes are found on most islands, and earthquakes are extremely frequent, causing many local changes in topography (Mawson, 1905, pp. 432-433, and Speiser, 1913). An interesting example is seen on Tanna, where a sea-level rock on which Captain Cook stood in 1774 has been subsequently elevated sixty feet (Mawson, 1905, p. 430, and Allen, 1922, p. 157).

Apparently there have been substantial changes in the size of the islands. Malekula has been relatively stable since Late Miocene or Early Pliocene times, but Vate and Espiritu Santo show Miocene and Pliocene outcrops at 1,000 and 2,000 feet, respectively. The *raised* Miocene deposits on the New Hebridean Islands present an intriguing correlation with the *sunken* Miocene deposits at Bikini and substantiate the theory that Micronesia has subsided and Melanesia been elevated during the Tertiary (Emery, Tracey and Ladd, 1954, pp. 152-154). The extent of subsidence in Micronesia is unknown, but the Eniwetok core drillings went through 4,222 feet of coral limestone before reaching base rock. Dobrin and Perkins (1954, p. 503) suggested that a minimum of 3,000 and a maximum of 13,000

feet of limestone, which was deposited in shallow water, underlie Bikini Atoll.

Without more geological study, the age of the New Hebridean area and the present islands cannot be determined. New Zealand and New Caledonia have long histories of elevation followed by partial subsidence, and Saipan in the Marianas appeared as volcanoes in the Eocene (Cloud, Schmidt and Burke, 1956, pp. 1, 20, 98). The biological data presented below strongly suggest that dry land has persisted in the New Hebridean region for long geological periods.

### Systematic Methods

Early in this study it became evident that there are several important differences between the systematic concepts and procedures of vertebrate zoologists and those of many malacologists. Since my zoogeographic conclusions are based primarily on molluscan evidence and this depends on the systematics, a brief statement of taxonomic theory seems necessary. Some of the material is a repetition of general systematic papers of the last few years, but it serves as a background for what may seem unorthodox.

#### IDENTIFICATION AND NOMENCLATURE

Involved in systematics are several often quite independent disciplines: identification, nomenclature, the study of speciation, and classification. Identification need concern itself only with the identity of an organism with a reference specimen, figure, or description. Nomenclature is the attempt to apply a static legal system in naming dynamically changing entities. When over-zealously applied, absurdities can occur such as dating the name of a *species* from the time and author of a "valid emendation" of a *name* (see p. 143). Use of priority and definite rules for generic and specific names are necessities, but placement of family and ordinal names under priority and type concepts results only in confusion and is not accepted here. H. B. Baker (1956a, b) "hastily reviewed" the retroactive effects of this ruling on the land snail family names and I follow his lead in refusing to accept the immediately indicated changes, much less those which could be dragged from the back shelves of libraries. In phyla where family level taxonomy is stabilized, application of priority might be advisable, but in the fluid state of land snail taxonomy, it is unacceptable.

## SPECIATION

*Types of species.*—No fully adequate definition of a species is available, but most systematists would agree that species seem “to be definable as distinct self-perpetuating units with an objective existence in nature, and therefore on a different theoretical footing from genera or families or other higher categories, which are not definable in this concrete way.” (Huxley, 1940, p. 4.) In the study of species (speciation) perhaps three arbitrary levels can be recognized: the typological or nomenclatural species, the morphologic species, and the biologic species.

The nomenclatural or typological species is based on the study of individuals and on the belief that species are “kinds.” The logical acme of the typologists in malacology came in the last half of the nineteenth century. Reeve, the Sowerbys, Bourguignat, Locard, and others named every variation as a species. The shattering of the two species of *Anodonta* (a fresh-water clam) found in France into 251 “species” may serve as an extreme example (see Mayr, Linsley and Usinger, 1953, p. 86). Most Pacific Island land snail species are “nomenclatural,” and prior to this study nearly all the New Hebridean “species” had been named by nomenclatural systematists.

The “New Systematics” focused attention on populations rather than individuals and the early attempts of Sarasin and Kleinschmidt to understand geographic variation have been brought to fruition in the studies of Rensch, Huxley, Mayr, and many others. Utilizing the conclusions of geneticists in regard to populations, they have tried to delimit species through the study of variation in morphologic characters. In birds and mammals, which have few species per student, the process of descriptive morphological systematics is well advanced; in mollusks and insects, with many species per student, it has barely begun. The criteria for species remain morphological, but a biological basis is assumed, since species are groups of populations that are actually or potentially capable of interbreeding under natural conditions.

Careful study of many “morphologic species” has revealed the presence of “biologic races” which are reproductively isolated under natural conditions and are distinguished by behavioral or genetic rather than morphologic characters. The taxonomic treatment of such “races” is one of the great problems facing biologists. Botanists partially resolve the problem by recognizing different types of species—morphologic “Linneons” and ecologic “elementary species.” Biosystematics or experimental taxonomy has been primarily de-

veloped by botanists, but many of the concepts are now being utilized by zoologists.

*Subspecific variation.*—In taxa where speciation has been thoroughly studied, modern systematic effort is directed toward interpretation of variation within species. Nomenclaturally, groups of populations within species are termed subspecies and are usually based on minor morphological differences. Edwards (1954, pp. 12–13) listed several types of subspecies, but common usage implies only geographic variation. Each subspecies occupies a definite geographic area and *most* specimens can be distinguished from *most* specimens of the adjacent subspecies. Occasionally, as in the pocket gopher, *Thomomys bottae*, with more than 150 “subspecies,” each local population is nomenclaturally recognized. Subspecies are often based on artificially isolated segments of uniform clines (see Wilson and Brown, 1953) and then serve no useful purpose. For emphasizing the breaks in “step-clines,” or striking “insular” variations, the subspecies, used cautiously, can be a helpful tool. For gradual morphologic trends in species, the nomenclaturally neutral “cline” is perhaps more suitable.

Study of the variation of Pacific Ocean land snails is practically synonymous with the work of Crampton (1916, 1925, 1932) on *Partula*. Besides his monumental efforts, only the papers of Neal (1934) on Hawaiian Helicinidae and the many papers of Powell (see References) on New Zealand *Paryphanta* are important. Research on snails from other areas of the world has provided certain “principles of variation” which are referred to throughout this text. In the New Hebrides different aspects of land snail variation can be directly correlated with the rainfall differential, altitude, frequency of topographic changes caused by earthquakes, and ecological stratification.

Effects of moisture and climate: Many land snails, particularly the prosobranchs, are very sensitive to reduced moisture supply, and the occurrence of populations of dwarfed individuals in local areas with reduced rainfall is very well documented. Shells of *Gonatoraphe fornicata* (Pfeiffer) from Espiritu Santo are very large, while those from Aneiteum are much smaller. Shells from the Port Vila, Vate, populations of *G. fornicata* and *Pleuropoma articulata* (Pfeiffer) are smaller than those from Aneiteum, but Vila is in the rain shadow of Mount MacDonal and probably has less rainfall than Aneiteum. The difference between the shells from the three islands is only in size, not in sculpture, shape, or other characters. Adopting the “75 per cent rule,” the populations, on size alone, would be sub-

specifically, if not specifically, "distinct." Yet the variation only reflects local physical conditions of the years the specimens were collected and, by itself, has no evolutionary significance. In the case of *Trochomorpha bakeri* Solem from Aneiteum, the xeric adaptations of heavier, thicker shell, lighter color, and more prominent sculpture are joined by the taxonomically important character of color band position. Specific separation from the Espiritu Santo *T. rubens* Hartman is therefore justified. The *Partula* and *Placostylus* of the southern islands show similar xeric adaptations, sometimes with systematically important differences, sometimes without.

Snails from the bottom of a valley will often be quite different in color, shape, and size from those found near the top of the hills. The correlation is with altitude, but the causative factor probably is moisture conditions in the micro-habitats. The slopes of a valley dry out much more quickly than the bottom, and snails near the top can be active for shorter periods of time than those at the bottom. The latter are usually bigger, more colorful, and with thinner shells. Often the height of the spire varies with altitude (see Solem, 1955). In the New Hebrides, "high altitude" specimens of *Partula* and *Diplomorpha* had higher spires than "low altitude" examples. In *Placostylus*, however, the reverse was true. The differences were large enough to be "subspecific" and many of the variations have been called "species" by typological systematists. Such variations reflect local conditions and I do not consider them worth nomenclatural recognition.

Effects of topography: The influence of local topography on variation of land snails is extremely important. Minor geographic obstacles are major dispersal barriers to snails, and local morphologically distinct populations, sometimes occupying a few square yards or a single tree, can develop. Examples of this are seen in the Hawaiian *Achatinella*, the Society Island *Partula*, the Cuban *Urocoptis*, and the Florida *Liguus*. For speciation to occur, however, relatively long term maintenance of the isolating mechanisms is necessary. In many land snail taxa, geographic isolation has been followed by speciation because of the snail's inability to cross filter zones. In some families, local colonies are effectively isolated from their neighbors, but relatively frequently the individual snails are mechanically dispersed by storms, winds, etc. There is, at irregular intervals, sudden mixing of morphologically distinct breeding populations, a period of amalgamation and formation of a new local "subspecies," chance dispersal resulting in another mixing of races, and so on, indefinitely.

This is apparently the normal course of events for fresh-water snails and the land snails which live near the strand line of the ocean. Passage of time results in so many gene exchanges between populations, essentially in a random manner, that the classical concepts of geographic speciation are inapplicable (for example, see Mayr and Rosen, 1956, on the West Indian *Cerion*).

In the New Hebrides, *Pleuropoma articulata* (Pfeiffer) and possibly *Omphalotropis (Oriella) setocincta* (Ancey) closely correspond to *Cerion* in habitat and variability, while the fresh-water planorbid, *Physastra layardi* (Ancey), shows a range of variation which encompasses ten of the New Caledonian "species" (see Franc, 1957, pl. 9, figs. 111-118). *Placostylus* shows similar variability. In New Zealand (Powell, 1947, 1951) and New Caledonia (Pain, 1955), *Placostylus* forms local morphologic races ("subspecies"), but in the New Hebrides there seems to be only bewildering variation (see pp. 132-135). The frequent earthquakes which change local topography provide a mechanism whereby morphologically divergent races can intermingle, hybridize, and produce extreme intra-population variability. If time permits, a stabilized morphotype can develop before the united populations are mixed with yet a third, or the variation can be increased by addition of yet another set of characters to the gene pool. I suspect the New Hebridean *Placostylus* will be found to have local populations with stabilized morphotypes interspersed between populations showing every conceivable degree of variability.

The process of separation and reunion of populations has been discussed recently by Hubbell (1956). For the union of previously isolated populations he has coined the term "phylosynapsis," and for the situation of highly variable populations in a zone between two stabilized morphotypes, the term "mosaic-discordant intergradation." If we strictly follow Hubbell's latter definition, the New Hebridean *Placostylus* does not seem to represent a zone of variability between two stable populations, but rather a single zone of variation. Possibly the difference is in the factor of area size, since Hubbell's example was based on a North American grasshopper which varies only in central Florida, while the New Hebrides have no center of stable populations. The type of variation is the same, and the causative factors (earthquakes in the New Hebrides, Pleistocene sea-land fluctuations in Florida) are equivalent.

Effects of ecological stratification: Ecological stratification is common in many groups of animals, but it has not been emphasized in molluscan systematics. There are no true arboreal snails in the tem-



perate zones. A few species will ascend the trunks of trees, but their presence is only temporary. Only in the tropics has a rich and varied fauna of tree snails developed. The change from terrestrial to arboreal habitat has occurred in many families and the basic modifications accompanying the change were discussed by Pilsbry (1894, p. xiv). The phenomenon of sympatric ecological speciation (or subspeciation) is virtually unknown in vertebrates, but it is quite common in insects and probably also in land snails, although it has been rarely reported. Indications that this has happened or is happening in the New Hebridean land snails were seen in the Bulimulidae, Zonitidae, and Helicinidae. On Espiritu Santo, the terrestrial species *Placostylus salomonis* (Pfeiffer), *Trochomorpha rubens rubens* Hartman, and *Pleuropoma sublaevigata* (Pfeiffer) have their arboreal counterparts in *Placostylus bicolor* (Hartman), *Trochomorpha rubens convexa* Hartman, and *Pleuropoma albescens* (Hartman). On Erromanga there are two terrestrial and one arboreal *Placostylus*.

*Criteria for specific recognition.*—From the above discussion, it follows that a species of land snail can show many shell variations. Undoubtedly many of the variations are genetic rather than phenotypic, but the difference cannot be recognized in museum specimens. In the present study of New Hebridean snails, only the morphologic species concept could be utilized. Ecological notes with the Kuntz collection aided interpretation of the morphologic data but are most useful in indicating possibilities for field studies. In delimiting species, morphologic intergradation has been accepted as proof of specific identity, and variations in size, color, height of spire, thickness of shell, *by themselves*, are considered to be of little or no importance in separating species. A few "typological species" in *Aneitea*, *Partula*, and *Diplomorpha* are retained because insufficient material was available to prove intergradation between the "species."

I have recognized very few subspecies in this study. This is partially caused by lack of material from most of the islands, but mainly by my inclination not to use "subspecies" as a means of indicating variation obviously correlated with physical conditions of local areas. Populations on different islands are recognized as subspecies in the cases of *Orpiella retardata* (Cox) and *Dendrotrochus eva* (Pfeiffer), but only in the case of *Aneitea robsoni* Hoffmann are subspecies recognized on the same island. The line between subspecific and specific difference is nebulous. *Lamprocystis guttula* (Pfeiffer) and *L. mendañae* Solem are species because they are slightly more sharply differentiated than are *Orpiella retardata retardata* (Cox) and *O. r.*

*depressa* Solem. The variations and geographic ranges are parallel, but the taxonomic treatment is arbitrarily different.

#### CLASSIFICATION

Although there can be little doubt that certain species are more closely related than others, whether a taxon is a section, subgenus, genus, subfamily, or family is a matter of personal opinion on the part of any taxonomist. The degree of relationship of species is provable, but the relative value of a taxon in a taxonomic hierarchy is arbitrary.

*Meaning of genera.*—Every species has two names; the second indicates its uniqueness; the first is a collective term designating *relationship*. As emphasized above, the species has a “real” existence, but the genus is an artificial device for pigeon-holing relationships. Obviously no uniform agreement as to the use of the genus can be expected. Within any group of animals the genus can have the same importance and meaning, but it can have quite different meanings in different groups. Perhaps the only direct comparison which can be made is by means of the number of species per genus and this information is presented for several taxa in Table I. If Iredale is temporarily ignored, the fact that genera of mollusks are much larger than genera of vertebrates is self-evident. In any given geographic area, the number of niches available to land snails is much greater than the number available to vertebrates. This undoubtedly has influenced *both* specific and supra-specific evolution. It cannot be stated that genera of land snails are larger because of more “minor” evolution, since within the land snail genera many species groups are recognized as “subgenera” and “sections.” Even with the addition of these subgeneric units, North American land snails would have 4.5 species per taxon, instead of 7.7 species per full genus. Thus, in relation to numbers of species per unit, a section of land mollusks is still larger than a genus of vertebrates, and a genus of land mollusks is much, much larger.

Part of the difference reflects the state of taxonomic knowledge of land mollusks. Many more people have studied vertebrates than have studied land snails. Specific relationships are better known and usually have been nomenclaturally recognized. The ultimate result of this is seen in ornithology, where 10,000 generic names are available for 8,500 species of birds (Mayr, 1942, p. 286). In vertebrate systematics this trend toward monotypic genera has been largely reversed, but in malacology it is in full swing. In the marine cowry

Table I.—The Genus in Modern Systematic Usage Based on the Fauna of North America North of Mexico

| Group                          | Number of species | Number of genera | Species/genus | Authority                          |
|--------------------------------|-------------------|------------------|---------------|------------------------------------|
| Birds.....                     | 800               | 400              | 2.0           | Mayr (1942, p. 287)                |
| South Africa.....              | 865               | 620              | 1.4           | Mayr (1942, p. 286)                |
| World, est.....                | 8500              | 2600             | 3.27          | Mayr (1942, p. 287)                |
| Mammals.....                   | 377               | 141              | 2.7           | Burt and Grossenheider (1952)      |
| Fishes <sup>1</sup> .....      | 4137              | 1490             | 2.8           | Jordan, Evermann, and Clark (1930) |
| Great Lakes.....               | 172               | 94               | 1.8           | Hubbs and Lagler (1947)            |
| Mexican FW.....                | 179               | 102              | 1.8           | De Buen (1947)                     |
| Reptiles <sup>2</sup> .....    | 236               | 89               | 2.6           | Schmidt (1953)                     |
| Amphibians <sup>2</sup> .....  | 142               | 38               | 3.7           | Schmidt (1953)                     |
| Butterflies <sup>3</sup> ..... | 432               | 140              | 3.1           | Klots (1951)                       |
| Land snails.....               | 714               | 93               | 7.7           | Pilsbry (1948)                     |
| Japan.....                     | 669               | 105              | 6.4           | Kuroda (1953)                      |
| South Africa.....              | 615               | 69               | 8.9           | Connolly (1939)                    |
| New Zealand.....               | 262               | 43               | 6.1           | Powell (1946a)                     |
| Australia.....                 | 644               | 175              | 3.7           | Iredale (1937a, b, 1938)           |

<sup>1</sup> Includes marine fishes from Panama and north; also Central American freshwater fishes.

<sup>2</sup> Includes Lower California.   <sup>3</sup> East of Great Plains only.

snails (family Cypraeidae), Hidalgo (1906–7) recognized 222 species in the Linnean genus *Cypraea*. After twenty years of studying shells, Schilder and Schilder (1938–39) recognized 165 species with 361 subspecies. These were placed in three subfamilies with 26 genera and 21 additional subgenera. Allan (1956) elevated subgenera and subjective synonyms to generic rank and placed 170 species with 420 subspecies in 13 subfamilies with 61 genera. Allan's classification, with 2.79 species per genus, compares favorably in size to vertebrate genera, but it has been unanimously criticized in reviews by conchologists for its extreme splitting. Even the Schilders' classification, with 6.35 species per genus, is regarded by many conchologists as being based on too fine a series of generic distinctions.

*Generic classification in land snails.*—For the past thirty years the leading students of land mollusks—Pilsbry, H. B. Baker, Watson, Connolly, Thiele, Boettger, Odhner, and C. M. Cooke, to name a few—have deliberately retained large genera and indicated smaller divi-

sions by subgeneric and sectional categories. The subgenera and sections provide a detailed analysis of affinities which can also be interpreted by the non-specialist. Elevation of the sections and subgenera to genera "isolates" the species from their relatives and immeasurably increases the difficulties of the non-specialist who tries to use a systematic monograph to provide data for zoogeographic or biologic studies. The use of subgenera and sections is counter to the procedures of vertebrate zoologists, but, I believe, serves the function of demonstrating *relationship* much better than the multiplication of genera.

An important exception to this view of classification is seen in the many papers of Tom Iredale (1933-45). Iredale has published valuable checklists on the land mollusks of Australia, Papua, Lord Howe, and Norfolk Island, in which several hundred new generic names are proposed. Type species are always designated, but generic descriptions and comparisons range from inadequate to non-existent. One genus is described as "more like the former than the latter, and it is conchologically neither." (Iredale, 1933, p. 57.) Iredale considers that anything Australian is generically distinct and that even most families are endemic to Australia. In order to include Iredale's regions in my zoogeographic survey, drastic alterations of his classifications have been necessary. Iredale emphasizes differences; I emphasize relationships. Revision of his genera is based on the study of specimens in the University of Michigan Museum of Zoology and Chicago Natural History Museum. In the time available for this project, it has been impossible to do the careful comparative studies that Iredale neglected. The conclusions as to Iredale's genera are thus presented here in as arbitrary a fashion as Iredale originally described them. Many of Iredale's genera delineate groups of species, but they greatly overemphasize the differences in extra-limital relatives.

*Criteria for generic recognition.*—My criteria for generic recognition have been primarily morphological. An ecological basis (see Inger, 1954, pp. 194-199) is not possible with island snails because of ecological speciation. Wherever possible, ecological and anatomical data have been utilized, but very little information on Pacific land snails is available. Thus most of the genera are based on conchological criteria. The classical "generic" characters of spire height, shape, color, and size are often of little value in classification, but H. B. Baker (1938b, p. 6) emphasized that "positive shell-characters (e.g., definite shell sculpture, columellar folds or teeth) are very use-

ful in classification, but that negative ones (i.e., the convergence exhibited by smooth, featureless, or even vestigial shells) have been repeatedly produced in widely divergent groups and may mean practically nothing." In the absence of definitive anatomical studies, extra-limital relationships of the New Hebridean species have been determined by close similarities or by obvious geographic trends in these positive shell features. The detailed classifications will undoubtedly be changed when comprehensive anatomical and ecological studies are available, but it is hoped that they closely approximate reality.

*Criteria for family recognition.*—Supra-generic categories have been based on the criteria used in generic recognition. Families and orders are primarily evolutionary patterns rather than units with a few key characters, and minor deviations are too often allowed to over-ride major similarities. Discontinuous southern distributions are extremely common in land snails, although they are uncommon in birds and mammals. Iredale has created endemic families for the Australian elements, but his actions are rejected in this study.

## FAUNAL REVIEW

The classification followed below is adopted almost completely from the studies of Pilsbry, H. B. Baker, Watson, and Boettger, and the ordinal categories are quite different from those in Thiele (1929, 1931), Iredale (1937a et seq.), and Franc (1957). Since my classification has been taken from scattered studies, I have summarized briefly the bases utilized in recognizing orders of land snails, together with references to the pertinent literature. As background for the zoogeographic discussion, the distribution of several family groups not found in the New Hebrides is briefly summarized. While they are not directly related to the New Hebridean fauna, information about their distribution and history has bearing on the time and mode of origin of the New Hebridean land snails.

Under each family I have attempted to give a brief summary of its major diagnostic characters, distribution, and probable relationships, and the important references in the literature. Keys have been provided to aid in the identifications below family level. No keys have been provided to introduced species, or to the Partulidae and Athoracophoridae.

Complete synonymies are given for all species native to the New Hebrides, but only one or two key references for introduced or very wide-ranging forms. Following the literature citations are (1) local

and extra-limital distribution, (2) a list of material examined, and (3) remarks on the ecology, anatomy, variation, and typology of the species. Detailed descriptions of species have been omitted, since this is not primarily a study in speciation.

Data concerning the variation in many species have been presented in tabular form. All measurements are in millimeters; whorl counts were made to the nearest eighth. Shells more than 5 mm. in maximum size were measured with a vernier caliper to the nearest 0.1 mm.; specimens under 5 mm. were measured by a calibrated Whipple counting disc under  $28\times$  magnification.

### Class GASTROPODA Cuvier, 1798

Of the five molluscan classes, only the Gastropoda have invaded the terrestrial habitat. Several different branches have made the transition from water to land, but generally the Prosobranchia are marine (with some land and fresh-water forms), the Opisthobranchia exclusively marine (except for the very questionable Lake Baikal *Ancylodoris*), and the Pulmonata land and fresh-water (with a few marine taxa). The basic classification of the gastropods was established in the last century, but in the past fifteen years a series of papers have appeared which provide much new information on which a reclassification can be based. No synthesis is as yet possible, but many important ideas have been offered by the studies of C. M. Yonge on functional anatomy, Fretter (1943) on *Oncidiella*, Hubendick (1945) on the Basommatophora, Pilsbry (1948) on the land mollusks, Graham (1949) on the molluscan stomach, Knight (1952) on primitive fossil gastropods, Boettger (1954) on the "euthyneura," Morton (1955) on the Ellobiidae, and H. B. Baker (1955) on the Pulmonata.

The land prosobranchs represent only a small fraction of the species found in that subclass, and comments in this study are restricted to subfamilial classification. The Pulmonata, however, are considered in detail, since all of the major groups are found in the New Hebrides or adjacent areas. The division of the Pulmonata into Stylommatophora (land snails) and Basommatophora (fresh-water snails) recognizes basic adaptive radiations and is supported by morphological and physiological characters. Surprisingly, there is no single adequate discussion of the adaptive differences, although much information is contained in Boycott (1934, 1936) and Hopwood (1944, 1945).

Pilsbry (1948) established a third superorder, the Systellommatophora,<sup>1</sup> for three families usually included with the Stylommatophora: the Oncidiidae, Veronicellidae, and Rathouisiidae. These families differ from the other pulmonates in lacking any shell and mantle cavity, and in having the lung, breathing pore, excretory opening, and anus at the posterior end. The eyes are at the tips of the peduncles, as in the Stylommatophora, but there are separate gonopores, as in the Basommatophora. Ecologically, the three families have barely left the sea, since the Oncidiidae are primarily inter-tidal and the Veronicellidae and Rathouisiidae are restricted to very humid tropical areas.

The Systellommatophora seem to be a natural group, but there is controversy as to its place in the Gastropoda. Some authorities—Plate (1893), Colosi (1921), and Fretter (1943)—believe that they are opisthobranchs, while others—Hoffmann (1925, 1928, 1929a), Watson (1925), and Pilsbry (1948)—consider them pulmonates. Homologies of structure are still uncertain (see Odhner, 1917), and comparative studies on the anatomy, embryology, and life histories are needed. The Oncidiidae are the most primitive and show the closest affinities to the opisthobranchs. Fretter (1943) summarized the reasons for removing them from the Pulmonata, but neglected their similarity to the Veronicellidae and Rathouisiidae, which show distinctly pulmonate characteristics (see Hoffmann, 1925, pp. 326–338). Probably the three families are more closely related to each other than to either the main pulmonate or opisthobranch lines.

Division of the Systellommatophora into two orders, the Oncidacea (Oncidiidae) and the Soleolifera (Veronicellidae and Rathouisiidae), recognizes the important habitat difference (inter-tidal vs. land) and several structural adaptations probably correlated with the environmental conditions.

The Basommatophora were surveyed by Hubendick (1945), and his classification has been retained. It is generally believed that the Basommatophora are more primitive than the Stylommatophora and that the latter were derived from an "Urtyp" corresponding rather closely to some of the more primitive Ellobiidae. The Ellobiidae are the only land Basommatophora (see Morton, 1955) and they present many characters from which the basic stylommatophoran structures can be derived. Since the only New Hebridean Basommatophora

<sup>1</sup> The name Systellommatophora is equivalent to the Ditremata, Teletremata, Clasthurethra, Digonopora, and Gymnophila of authors. Strict priority would require use of Fischer's name, Ditremata, but since Pilsbry's name is in etymological conformity with the names of the other two superorders, it is here retained.

considered here are planorbid snails, no comments have been made on the supra-familial classification of the Basommatophora proposed by Hubendick (1945) and Morton (1955).

The Stylommatophora contain about 88 per cent of the New Hebridean Pulmonata. No system for classifying the Stylommatophora has gained universal acceptance. Those of Pilsbry (1900a, 1948), Pelseneer (1906), and Thiele (1931) are most widely used today; the older systems of Mörch, Semper, Fischer, and others have only historical interest.

Pelseneer (1906) established four divisions: the Ditremata (= Systellommatophora), Elasmognatha (= Heterurethra and Tracheopulmonata), Agnatha (the carnivorous snails), and Holognatha (remaining families). This system was based on the number of gonopores and the structure of the jaw. It failed to provide any concept of relationships between the many families of the Holognatha and overemphasized the phylogenetic importance of the carnivorous habit. Watson (1915) showed that carnivorous snails have developed in several different families and that the characters of Pelseneer's Agnatha are the result of convergent evolution.

Thiele (1931) divided the pulmonates into a number of "Stirpes" or superfamilies, but his classification gave no indication of any relationships between them. As part of the only general classification of the Mollusca to appear since Pelseneer (1906), undoubtedly Thiele's system will be widely used in regional studies. It has already been partially adopted by Iredale (1937a, 1938, 1941) for Australia and Papua, by van Benthem Jutting (1948, 1950, 1952, 1953a, 1956) for Java, and by Franc (1957) for New Caledonia. Despite many excellent innovations, much of Thiele's classification of the Stylommatophora is faulty and it has been criticized by several malacologists (Pilsbry and Cooke, 1934a; H. B. Baker, 1938b, 1941; and Pilsbry, 1948). Several of Thiele's "Stirpes," i.e., Zonitacea, Ariophantacea, are clearly heterogenous. Much of Thiele's classification below family level has been utilized here, but his higher categories have not been accepted.

The most comprehensive classification of the Stylommatophora has been developed by Pilsbry (1900a, 1919, 1948) and H. B. Baker (1955, 1956a, b). Based on the structure of the pallial region, five orders—Heterurethra, Tracheopulmonata, Orthurethra, Mesurethra, and Sigmurethra—have been recognized. Originally Pilsbry separated the Tracheopulmonata from the typical Stylommatophora because of the peculiar structure of the lung in this group. Baker



(1955) suggested that the Tracheopulmonata are closely related to the Heterurethra, but the subject needs more investigation. Use of the pallial organs as primary criteria for ordinal recognition was criticized by Simroth and Hoffmann (1908-28, pp. 408, 1223-24), Wächtler (1934), and Thiele (1935, p. 1064). Their objections were based on variations in the position of the ureter, which seemed to form a series of transitions between the ordinal categories; in one case these variations occurred in a single family (see Wächtler, 1934, for a bibliography). Without more study, it is impossible to determine the importance of the pallial regions in pulmonate classification. I consider that the cited variations will probably be found to be secondary modifications of the basic plan, and thus will not affect the usefulness of the criteria in recognizing the ordinal categories. Most American authors, and three European malacologists—Watson (1915, 1920), Steenberg (1925), and Boettger (1952, 1954)—have adopted Pilsbry's classification.

The "key character" used in separating the various orders is the relationship of the ureter to the kidney and other pallial organs. Briefly, the five orders are characterized as follows:

Heterurethra: Ureter along front margin of kidney, then following rectum to pneumostomal opening (fig. 1, *a*).

Tracheopulmonata: Ureter multi-looped, opening into respiratory pore or directly to exterior (fig. 1, *b*).

Orthurethra: Ureter remote from hindgut, running from tapered anterior end of kidney to anterior border of lung (fig. 1, *c*).

Mesurethra: Ureter represented mainly by lateral opening of the relatively short kidney (fig. 1, *d*).

Sigmurethra: Ureter abruptly reflexed, passing to posterior end of lung cavity, then turning across to the last fold of the gut and following it forward to the mantle edge (fig. 1, *e*).

During the evolutionary change from a shell-bearing snail to a "Halbnacktschnecke" or a slug, the pallial region may become greatly altered in position, size, and organization. Thus, the many slug taxa do not seem to follow the above criteria, but must be related to ordinal categories through their affinities with shell-bearing snails, rather than on their own characteristics. When the nearest generic relatives are unknown, great confusion can result. For example, the genus *Aillya* is known from the Cameroons and Fernando Po (fide Watson). Odhner (1927) described the anatomy of *Aillya* and placed it in the Amphibuliminae (family Bulimulidae) on the basis of the radula, jaw, anal pouch, and stomach. He noted, however, that the structures of the nephridium, genitalia, intestine, and spermathecal

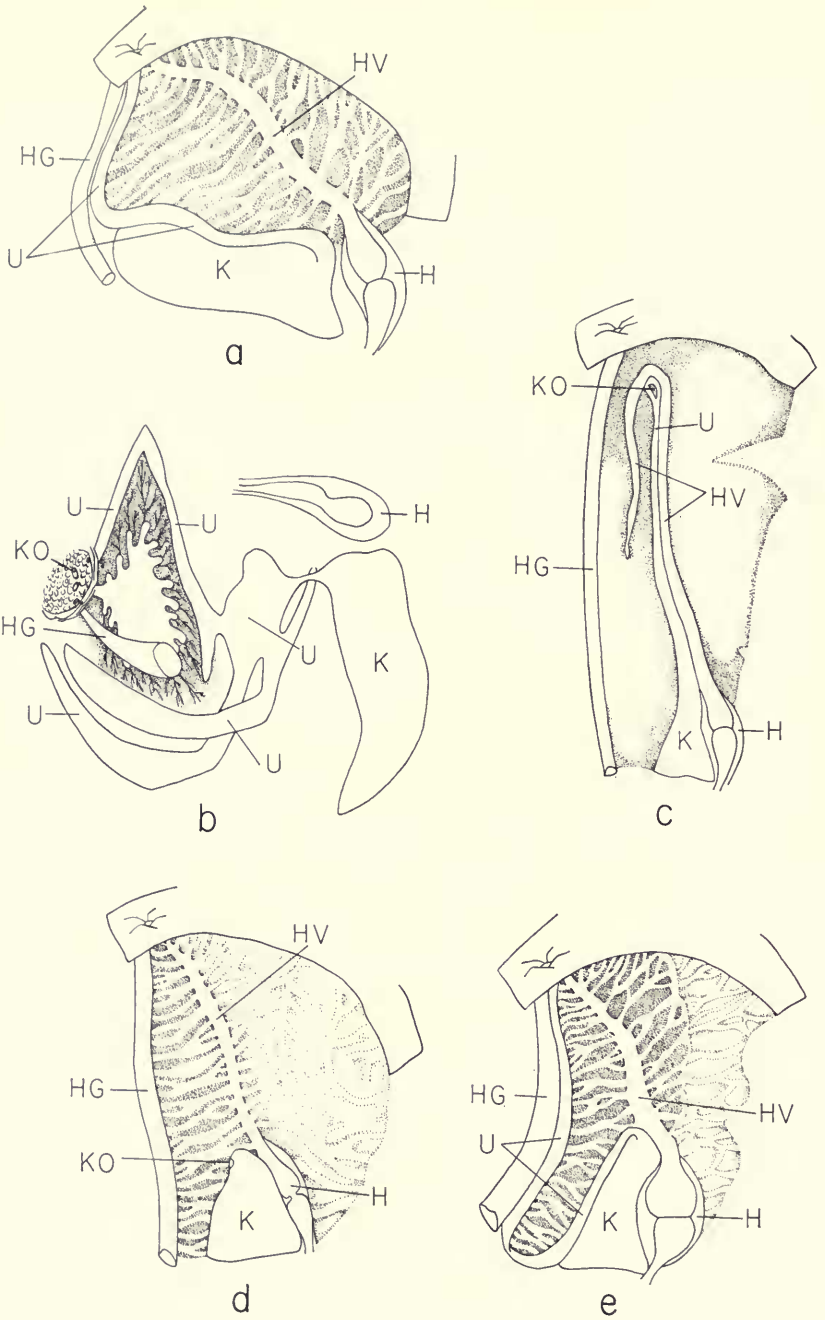


FIG. 1. Pallial organs of stylommatophoran snails: *a*, Heterurethra; *b*, Tracheopulmonata; *c*, Orthurethra; *d*, Mesurethra; *e*, Sigmurethra (after various sources). Kidney (K), ureter (U), renal orifice (KO), hindgut (HG), principal pulmonary vein (HV), heart and pericardium (H).

stalk are similar to those of the Succineidae, while the ureter is partially transitional between the types found in the Succineidae and Athoracophoridae. Pilsbry (1946b) thought that *Aillya* might be an aberrant zonitid snail (Sigmurethra, Aulacopoda), and H. B. Baker (1955, p. 110) placed it in the Heterurethra. Similarly the genus *Ceciliodes* was of uncertain position before Watson's study (1928). Such examples of the difficulty in classifying particular genera have been used by many conchologists (students of shells) as an excuse for ignoring the importance of the soft parts in systematics and for rejecting the conclusions of malacologists (students of shells and soft parts).

Little can be said about the relationships between the ordinal categories. The pallial region of the Basommatophora is most similar to that of the Orthurethra (fig. 1, *c*), and Pilsbry (1900a, et seq.) considered the Orthurethra to be the most primitive order of the Stylommatophora. The Heterurethra (Succineidae or amber-snails) and Tracheopulmonata (the slugs of the family Athoracophoridae) have quite different pallial regions (fig. 1, *a, b*) but the importance of this difference is unknown. The multi-looped kidney and "tracheal" lung of the Athoracophoridae are distinctive, but somewhat similar variations have been produced in other slug taxa. H. B. Baker (1955, p. 110) pointed out parallelisms in both the Veronicellidae and Ancyliidae and placed both the Aillyidae and Athoracophoridae in the Heterurethra. Without more study of the taxa involved, including the aberrant succineids *Omalyonyx* and *Hyalimax*, I prefer to retain the Heterurethra and Tracheopulmonata as separate categories. If their union proves justified, the name *Elastomognatha* Mörch should be applied to the combined category, since it was originally proposed to cover both the Succineidae and Athoracophoridae.

Baker (1955) suggested that the Sigmurethra were derived from a heterurethrous and aulacopod ancestor, rather than from an orthurethran, but further study is needed. The Mesurethra represent a side branch from the main stream of pulmonate evolution and probably had no part in the ancestry of the dominant Sigmurethra. No members of the Mesurethra are found in the New Hebrides, but the order is zoogeographically important and a brief synopsis of its distribution and content is given (pp. 42-43).

Within the Sigmurethra two main lines of development have been recognized by establishing the suborders Aulacopoda and Holopoda. Proposed by Pilsbry (1896), these suborders are based on the rela-

tive position and prominence of the pedal grooves (see fig. 2). In the Aulacopoda they are conspicuously impressed and situated well above the margin of the foot; thus a part of the sole of the foot forms the lower portion of the side of the animal (fig. 2, *a*). In the Holo-

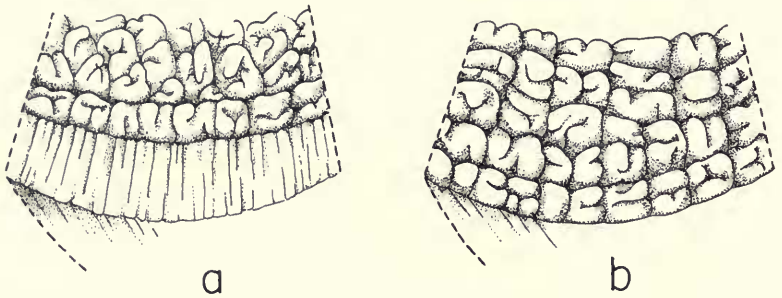


FIG. 2. Pedal grooves in the Aulacopoda and Holopoda: *a*, aulacopod type (from *Hemiplecta neptunus* Pfeiffer; CNHM 33041); *b*, holopod type (from *Zachrysia guanensis* Poey; CNHM 53481).

poda the grooves are rather inconspicuous and are at or close to the angle of the foot (fig. 2, *b*). Wächtler (1935) reviewed the morphology of the gastropod foot and concluded that the position of the pedal grooves was characteristic, at least for families. He was uncertain as to the value of the Aulacopoda and Holopoda as primary divisions but perhaps was confused by the variation in other orders, since he had previously (1934) rejected the Heterurethra-Orthurethra-Sigmurethra concept of Pilsbry (1900a). Pilsbry (1946b, pp. 231-232) admitted that in a few cases the distinction between the Aulacopoda and Holopoda becomes blurred, but he considered the separation valid. The Aulacopoda are the more primitive and are more important in the faunas of the southern hemisphere than in those of the northern. By far the largest number of species of land snails belong to the Holopoda.

### Subclass PULMONATA Cuvier, 1817

#### Superorder SYSTELLOMMATOPHORA Pilsbry, 1948

Pulmonata with eyes on contractile (Soleolifera) or inversible (Oncidiacea) stalks. Body oval or lengthened, slug-like. Convex or keeled dorsal integument without mantle cavity or shell, extending down over head on all sides. Lung posterior, breathing pore, anus, and nephridial pore behind foot. Male genital opening at right side of head; female opening midway on right side of hyponotum or near anus. (Modified from Pilsbry, 1948, p. 1062.)

Order ONCIDIACEA Thiele, 1931<sup>1</sup>

Shell-less animals with one pair of tentacles bearing terminal eyes. Mouth surrounded by large sensory lobes. Radular teeth unicuspid. Respiration by lung and branchial gills. Male gonopore at right side of head, either inside or outside right tentacle; female gonopore at posterior end of body near anus.

## Family ONCIDIIDAE

The studies of Semper (1885), Plate (1893), Watson (1925), Hoffmann (1928, 1929a), H. B. Baker (1938a), Fretter (1943), and Awati and Karandikar (1948) summarize present knowledge of the family and provide a guide to the vast literature. Oncidiids are found in all oceans from 60° N. to 55° S. but are most numerous in the oceans of the triangle formed by the Andamans, the Philippines, and New Caledonia.

Most Oncidiidae live in the tidal zone. A few are terrestrial (Fretter, 1943, p. 716, and Hoffmann, 1932, p. 134), while others inhabit brackish water (Plate, 1893). Oncidiids have pelagic larvae and are distributed like marine organisms, but are included here because of their pulmonate affinities.

The only New Hebridean Oncidiidae available to me were found in a marine tidal zone on Espiritu Santo by G. S. Banner in 1943. Except for a record by Bretnall (1919), they are the only oncidiids known from the New Hebrides. Of the six genera of Oncidiidae, *Oncis* and *Oncidium* are known from the islands, while *Oncidina* probably will be found there. The classification of the Oncidiidae is based on the internal anatomy, but the New Hebridean species can be identified from external characters (see pl. 3, fig. 2). The following key includes *Oncidina australis* Semper, as well as the species actually examined.

## Key to the New Hebridean Oncidiidae

1. Dorsal eyes present, either singly or in groups; hyponota present . . . . . 2  
    Dorsal eyes absent; no hyponota; no branchial plumes; sole and head reddish-gray . . . . . *Oncidina australis* Semper
2. Hyponota narrower than sole of foot; dorsal eyes arranged in groups; branchial plumes present; size large . . . . . 3  
    Hyponota wider than sole of foot; dorsal eyes single; branchial plumes absent; size small . . . . . *Oncis martensi* Plate

<sup>1</sup> If type concepts and priority are applied to ordinal categories, earlier names can be utilized. Since Thiele was the first to use a name of more than family rank for the Oncidiidae only, his name has here been accepted.

3. Branchial plumes distributed over entire notum; respiratory pore one-fourth to one-third width of hyponotum from anus, off median line; hyponota equal to greatest width of foot sole. . . . . *Oncidium peronii* Cuvier  
 Branchial plumes on posterior fourth of notum only; respiratory pore one-half to one-third width of hyponotum from anus, on median line; hyponota narrower than greatest width of sole. . . . . *Oncidium verruculatum* Cuvier

Genus **ONCIDINA** Semper, 1885

*Type species.*—*Onchidina australis* Semper.

**Oncidina australis** Semper

*Oncidina australis* Semper, 1885, *Reisen im Philippinen*, 3, (7), p. 287, pl. 19, figs. 11, 14, 15, pl. 21, fig. 27, pl. 23, fig. 10; Bretnall, 1919, *Rec. Australian Mus.*, 12: 325.

*Oncidina australis* (Semper) Plate, 1893, *Zool. Jahr., Anat.*, 17: 208, pl. 7, fig. 13, pl. 8, figs. 24, 35, pl. 10, fig. 51; Hoffmann, 1928, *Zool. Jahr., Syst.*, 55: 102.

*Range.*—Brisbane, Australia, New Caledonia, and Fiji.

*Material.*—No material available.

*Remarks.*—The range of this monotypic genus is such that it may be found in the New Hebrides. The absence of hyponota and dorsal eyes at once separate *Oncidina* from the other New Hebridean *Oncidiidae*.

Genus **ONCIS** Plate, 1893

*Type species.*—*Oncidina coriacea* Semper.

*Remarks.*—The thirteen species of *Oncis* range throughout much of the Indo-Australian region (Hoffmann, 1929a, p. 254). Although previously known from New Britain and Queensland, this is the first record from east of the 160th meridian.

**Oncis martensi** Plate

*Oncis martensi* Plate, 1893, *Zool. Jahr., Anat.*, 7: 196-197, pl. 7, fig. 7—Singapore (error); Martens, 1897, in *Weber's Zool. Ergeb. Ost-Indien*, 4: 128—Petshaburi, Gulf of Siam (correction of error); Hoffmann, 1928, *Zool. Jahr., Syst.*, 55: 89.

*Range.*—Espiritu Santo, Gulf of Siam, India.

*Material.*—Espiritu Santo (AMNH, G. S. Banner!).

*Remarks.*—The single juvenile specimen is most similar to *O. martensi* Plate and, pending study of adult individuals, is referred to that species. The specimen is only 7 mm. long and has six dorsal eyes, in comparison with the type, which is 66 mm. and has ninety dorsal

eyes. The unspecified Indian record is taken from Awati and Karandikar (1948).

Genus **ONCIDIUM** Buchanan, 1800

*Type species.*—*Oncidium typhae* Buchanan.

### **Oncidium peronii** Cuvier

*Oncidium peronii* Cuvier, 1805, Ann. Mus. Paris, 5: 37; Bretnall, 1919, Rec. Australian Mus., 12: 311—Lord Howe, Santa Cruz Islands.

*Oncidium tonganum* Quoy and Gaimard, 1832, Voy. Astrolabe, 2: 210, pl. 15, figs. 17–18—Tonga Islands.

*Oncidium peroni* (Cuvier) Hoffmann, 1928, Zool. Jahr., Syst., 55: 71–72.

*Range.*—Lord Howe, Santa Cruz Islands. From Red Sea and Mauritius to New Caledonia, Samoa, and the Marshall Islands.

*Material.*—No material available.

*Remarks.*—*Oncidium peronii* is the common species of Polynesia and since it has been found on all sides of the New Hebrides it undoubtedly lives there. *O. peronii* and *O. verruculatum* have often been confused. Numerous differences exist between the two (see Bretnall, 1919, and Hoffmann, 1928), the most obvious of which are given in the key.

### **Oncidium verruculatum** Cuvier

*Oncidium verruculatum* Cuvier, 1830, Reg. Anim., 2nd ed., 3: 46; Bretnall, 1919, Rec. Australian Mus., 12: 309–310.

*Oncidium verruculatum* (Cuvier) Hoffmann, 1928, Zool. Jahr., Syst., 55: 72–74; Awati and Karandikar, 1948, Univ. Bombay, Zool. Mem., no. 1, 52 pp., 62 figs.

*Range.*—Espiritu Santo, Africa to Japan, New Guinea, Australia, and New Caledonia. Also common in Hawaii, but not known from Polynesia.

*Material.*—Espiritu Santo (AMNH, G. S. Banner).

*Remarks.*—Branchial plumes are developed in the one adult and smallest juvenile but are lacking in the other five specimens. All have groups of dorsal eyes, fourteen groups of two to six eyes in the adult and three to eight groups of two to four eyes each in the juvenile specimens. Awati and Karandikar (1948) give an excellent summary of our knowledge of this species. Their findings contradict the observations of Fretter (1943) on *Oncidiella* and suggest pulmonate rather than opisthobranchiate affinities for the Oncidiidae. Further study is needed to resolve the differences.

Order **SOLEOLIFERA** Simroth, 1890

Slug-like mollusks without external or internal shell. Head bearing two pairs of tentacles, the upper ommatophores, the lower tactile. Radular teeth unicuspid. Male genital opening at right side of head, female opening in pedal groove or hyponotum about midway along right side of body.

The Veronicellidae are herbivorous, the Rathousiidae carnivorous, and the characters separating the two families which comprise the Soleolifera primarily reflect this dietary distinction. In the Rathousiidae the jaw is lacking; the female gonopore is in the pedal groove; the genital organs lack accessory glands; the radular teeth are slender and dagger-shaped; and, in the Austro-Melanesian species, the notum is sharply rounded or keeled (see Laidlaw, 1940).

Rathousiids (fig. 17) are known from southeast China, Tonkin, Siam, Burma, Malaya, Indonesia, the Philippines, New Guinea, the Bismarcks, and northern Queensland (see Hoffmann, 1925). Probably both rathousiids and veronicellids will be found in the Solomon Islands, although no slugs have been reported from the islands up to the present time.

Family **VERONICELLIDAE (=Vaginulidae)**

Terrestrial slugs without internal or external shell. Rounded dorsal surface covered by mantle (or notum) and separated from ventral surface by a sharp keel, the perinotum. Ventral surface with central sole, separated from the lateral hyponota (which are ventral continuations of the notum) by a pedal groove. Head with four tentacles, the upper pair having terminal eyes. Head and tentacles of contracted specimens hidden beneath notum. Female gonopore about midway in right hyponotum. Male gonopore at right side in groove between mouth and foot. Jaw low, arcuate, formed of narrow vertical plates. Radula with narrow central and broad lateral teeth, all unicuspid. (Adapted from Pilsbry, 1948, p. 1062 and van Benthem Jutting, 1952, pp. 327-328.)

Hoffmann (1925) discussed the systematics, anatomy, zoogeography, and phylogeny of the Veronicellidae. Unfortunately his nomenclature is incorrect, and H. B. Baker (1925a, 1931) should be consulted in conjunction with this otherwise excellent contribution. The Veronicellidae have a circumtropical distribution which closely approximates that of the palm trees except in North Africa and the Middle East, where no veronicellids are found. The slugs live under stones, grass tufts, or decaying wood and feed on living or decaying plants. Occasionally they assume economic importance through the destruction of crops.

Collinge (1900), Grimpe and Hoffmann (1925a, b) and Hoffmann (1929b) studied New Hebridean veronicellids. Two genera, each



represented by a single species, have been reported from the islands. Both the South American *Angustipes* and the Indonesian *Eleuthero-caulus* were probably introduced. I have seen no specimens and the information presented below has been abstracted from the literature. Material from Vate Island is particularly desirable to determine if *V. brunnea* Collinge is a synonym of *A. plebeius* (Fischer) as reported by Grimpe and Hoffmann (1925a).

### Genus *ANGUSTIPES* Colosi, 1921

(= *Belocaulus* and *Sarasinula* of Grimpe and Hoffmann, 1925a)

The South American *Angustipes* differs from the African *Imerinia* in lacking a doubled spermatheca (H. B. Baker, 1931, p. 136). *Angustipes* s.s. (= *Belocaulus*) usually has the greatest width of the verge below the middle and the verge is without an "S"-shaped curve.

### Section *SARASINULA* Grimpe and Hoffmann, 1925

*Type species*.—*Vaginula grandidieri* Crosse and Fischer.

### *Angustipes* (*Sarasinula*) *plebeius* (Fischer). Plate 3, fig. 4.

*Vaginula plebeius* Fischer, 1868, Jour. de Conch., 16: 145-146—Noumea, New Caledonia.

*Vaginula brunnea* Collinge, 1900, Willey's Zool. Results, 4: 435, pl. 41, figs. 18-23—Vate, New Hebrides.

*Vaginula hedleyi* (Simroth) Collinge, 1900, op. cit., p. 435—Vate.

*Sarasinula plebeja* (Fischer) Grimpe and Hoffmann, 1925, Nova Caledonia, 3, (10), pp. 357-362, 365-366, pl. 6, figs. 1-3—Malo, New Hebrides.

*Imerinia plebeja* (Fischer) Hoffmann, 1929, Zool. Anz., 84, (5-6), p. 117—Espiritu Santo.

*Angustipes* (*Sarasinula*) *plebeius* (Fischer) H. B. Baker, 1931, Nautilus, 44, (4), pp. 134-136.

*Range*.—Vate, Malo, and Espiritu Santo. Also known from New Caledonia, Loyalty Islands, Queensland, Fiji, Samoa, Tahiti, Mascarene Islands, Trinidad, Antigua, St. Thomas, Rio de Janeiro and Bahia, Brazil.

*Material*.—No material available.

*Remarks*.—Hoffmann (1927, p. 35) united *A. plebeius* with the Brazilian-Antillean *A. dubia* (Semper). Both Hoffmann and Baker attest to the pan-tropical distribution of this species. Baker considered that it was introduced into Polynesia during historical times.

Genus **ELEUTHEROCAULUS** Simroth, 1913

(= **Laevicaulus** Simroth, 1913, and **Meisenheimeria** Grimpe and Hoffmann, 1925)

*Type species.*—*Vaginula comorensis* Fischer (= *V. alte* Ferussac).

**Eleutherocaulus alte** (Ferussac). Plate 3, fig. 3.

*Vaginula alte* Ferussac, 1823, Hist. nat. Moll. terr. fluv., 2: 96—Pondicherry.

*Veronicella leydigii* (Simroth) Collinge, 1900, Willey's Zool. Results, 4: 435—Vate, New Hebrides.

*Meisenheimeria alte* (Ferussac) Grimpe and Hoffmann, 1925, Nova Caledonia, 3, (10), pp. 362–367, pl. 4, figs. 4–6.

*Laevicaulus alte* (Ferussac) Hoffmann, 1929, Zool. Anz., 84, (5–6), p. 117; van Benthem Jutting, 1952, Treubia, 21, (2), p. 330.

*Range.*—Vate(?). East Africa to the Philippines and Tenimber Islands, Queensland, New Caledonia, and the Loyalty Islands.

*Material.*—No material available.

*Remarks.*—Collinge's record from Vate Island needs confirmation, but it is probably correct.

Superorder **STYLOMMATOPHORA** Schmidt, 1855

Snails with eyes on tips of a pair of superior invaginable tentacles and with a smaller inferior pair of feelers which are rarely (Athoracophoridae and some Pupillidae) lacking. Animal hermaphroditic, with a common external gonopore (rarely narrowly separated) opening near the right tentacle. Shell external, varying from large (helices) to vestigial (*Testacella*), or internal and consisting of a calcareous plate or series of fragments (except in the Philomycidae where the shell is completely absent). Pallial cavity without ctenidia and respiration primarily through a more or less heavily veined lung. All are terrestrial.

Of the five orders of the Stylommatophora, only the Mesurethra is not found in the New Hebrides. The Heterurethra and Tracheopulmonata are represented by only one or two species and the Orthurethra by probably not more than ten; the great majority of the species belong to the Sigmurethra. The Heterurethra and Tracheopulmonata never form a large element in a fauna, and only on Rapa and the Hawaiian Islands do the Orthurethra become dominant. In all other regions of the world, various sigmurethrous taxa have the greatest numbers of species.

The order Mesurethra was created by H. B. Baker (1955) for the relict land snail families Cerionidae, Corillidae, and Acavacea. The Cerionidae are West Indian and live only on the portion of the sea shore that is above high tide but is reached by salt spray. The

Corillidae are found in India, China, southeast Asia, and Ceylon, with a few representatives in South Africa. The Acavacea include genera from South America, South Africa, Madagascar, the Seychelles, Ceylon, Tasmania, New South Wales, and Queensland. The shells are very different in appearance, but anatomical structures indicate their close relationship. The conchological dissimilarity led Iredale (1937b, pp. 14-19) to create four families and seven genera for the thirteen Australian species. Watson (*in* Connolly, 1915), Germain (1925) and Boettger (1936) reviewed the phylogeny of the Acavacea. They recognized four subfamilies (or families): the Strophocheilinae, Acavinae, Dorcasiinae, and Caryodinae. The Strophocheilinae of South America are the most primitive, the Acavinae of Ceylon, the Seychelles, and Madagascar the most advanced. The Dorcasiinae from South Africa and the Caryodinae from Australia and Tasmania are intermediate in the possession of primitive characters. In each area the primitive genera are more southern in distribution, and the more advanced are northern. The distribution has been interpreted by Watson and Germain to indicate an origin for the Acavacea in the "Gondwana" area.

### Order TRACHEOPULMONATA Simroth, 1890

Animal without external shell. Integument with furrows outlining a triangular head shield and a usually triangular mantle on right side of animal. Head with two eye-bearing invaginable tentacles. Lung with trachea-like air spaces. Kidney with highly convoluted ureter. Jaw elasmognathous. Radula with central tooth well developed, vestigial, or lacking. One or more calcareous bodies present beneath mantle shield. (Adapted from Thiele, 1931, p. 494.)

The highly unusual pallial system of the Tracheopulmonata has been carefully studied by Plate (1897), W. Pfeiffer (1900), and Glammann (1903). Although they worked with different genera, their conclusions agree except in minor details. Plate (1897) compared the lung structure of *Athoracophorus* to the tracheal system of insects, but most probably it is only a highly specialized "Gefässlung" (see Simroth, 1918). Equally interesting is the multi-folded ureter (see fig. 1, b) which forms one of the primary reasons for regarding the Tracheopulmonata as a separate order.

The single family, the Athoracophoridae (fig. 18), is restricted to New Guinea, Queensland, New South Wales, the Bismarcks, the Admiralty Islands, the New Hebrides, New Caledonia, and New Zealand. Probably species will be found in the Solomon Islands.

Family **ATHORACOPHORIDAE (=Janellidae)**

Many generic names have been proposed for athoracophorids, but I am recognizing only four genera. Simroth (1918) described two genera, *Ottonita* Strand, 1932 (= *Ottonia* Simroth, 1920, *non* Gistel, 1848), and *Neomecklenburgia*, from the Bismarcks, but their status is uncertain. Grimpe and Hoffmann (1925a) were unable to determine their validity, and until new material becomes available they are better left as dubious taxa.

*Athoracophorus* Gould (fig. 21, B) is restricted to New Zealand and the neighboring islands (see Suter, 1913). The rachidian tooth is large, with four to seven denticles, and the lateral teeth normally have six to seven cusps. The notum is deeply furrowed and there is much variation in the shape and relative positions of the mantle and cephalic shields. All species of *Athoracophorus* have the notum separated from the foot sole by a narrow hyponotum. Powell (1946a) placed the New Zealand species in four genera. The differences between these "genera" are much smaller than those between the New Zealand species and the other genera. A better understanding of the importance of the radiation in New Zealand is obtained by reducing Powell's genera to subgenera and sections of *Athoracophorus*.

*Aneitea* Gray (fig. 21, C) is found in New Caledonia and the New Hebrides but has not been found in the Loyalty Islands. Specimens have evidently been introduced into the botanical gardens at Brisbane, Australia (*Aneitea brisbanensis* W. Pfeiffer, 1900). The central tooth is greatly reduced or absent and the lateral teeth have four cusps. The notum is deeply furrowed and the mantle and cephalic shields are clearly outlined and in contact with one another. *Triboniophorus* is similar in external appearance, but there are radular and anatomical differences.

*Triboniophorus* Humbert (fig. 21, A) is reported from Queensland, New South Wales, New Guinea, New Caledonia, and the New Hebrides, but the last two records are questionable.

*Aneitella* Cockerell (fig. 21, D) has been found on New Britain and the Admiralty Islands. The rachidian tooth is absent and the first two lateral teeth are partially fused. The notum is unfurrowed and the mantle and cephalic shields are only weakly outlined.

For the Athoracophoridae Grimpe and Hoffmann (1925a) postulated an Antarctic origin followed by two radiations. The first was from New Zealand to New Caledonia and the New Hebrides, the second from Australia to the Bismarck and Admiralty Islands.

This theory assumed that athoracophorids are absent from New Guinea and the Solomons and that *Aneitella*, without a rachidian tooth, is more primitive than *Athoracophorus*, which has a central tooth. Van Benthem Jutting (1933) reported *Triboniophorus* from the interior of New Guinea, and probably some species of Athoracophoridae will be found in the Solomon Islands. Possession of a rachidian tooth is a basic pulmonate character. Other factors being equal, *a genus with a well-developed central tooth is more primitive than a genus which is losing or has lost the central tooth.*

*Aneitella*, without a rachidian tooth, is thus less primitive than *Athoracophorus*. The loss of the skin furrows in *Aneitella* is another indication of its advanced status.

Much less difficulty is encountered if a northern origin is postulated for the Athoracophoridae, with New Guinea as the dispersal center from which the present genera were derived. *Athoracophorus* is the most primitive, *Triboniophorus* slightly less primitive, *Aneitea* specialized and *Aneitella* highly specialized. The most probable path of immigration would have been from New Guinea through the Solomons and New Hebrides(?) to New Caledonia and New Zealand. *Triboniophorus* was probably preserved in the highlands of New Guinea and only comparatively recently spread into eastern Australia. Whether the Athoracophoridae originated in New Guinea or spread there from southeastern Asia is unknown. Possibly advanced athoracophorids will be found in the Solomons and in the lowlands of New Guinea.

Two genera of athoracophorids have been reported from the New Hebrides. Glamann (1903) recorded *Triboniophorus* from an unknown locality, and *Aneitea* is an important part of the fauna.

#### Genus **TRIBONIOPHORUS** Humbert, 1863

Rachidian tooth large, with three to five cusps; lateral teeth usually with four cusps. Oviducal accessory gland near the albumen gland. Kidney crescent-shaped, ureter with four or five loops (Thiele, 1931, p. 495).

*Type species.*—*Triboniophorus graeffei* Humbert.

*Remarks.*—Hedley (1889) recognized only one species, although several names have been applied to the Australian specimens. Glamann (1903) made a histological examination of the pallial region of *Triboniophorus* and at the end of his paper mentioned that the specimen was from the New Hebrides. The validity of this record is doubtful and needs confirmation. Grimpe and Hoffmann (1925a) described *T. sarasini* from Mount Humboldt, New Caledonia, on

the basis of four specimens about 16 mm. long. I suspect that juvenile specimens of *Aneitea* rather than adults of *Triboniophorus* were involved. Van Benthem Jutting (1933, p. 90) reported specimens from Dutch New Guinea collected between 4,600 feet and 7,800 feet elevation. They were at most subspecifically distinct from the east Australian *T. graeffei*. The great amount of variation she found in the shape of the rachidian tooth of *Triboniophorus* supports my conclusions on *Aneitea* (see pp. 47, 50).

### **Triboniophorus graeffei** Humbert

*Triboniophorus graeffei* Humbert, 1863, Mem. Soc. Phys. Nat. Genève, 17, (1), p. 116—Wollongong, New South Wales, Australia.

*Aneitea graeffei* (Humbert) Glamann, 1903, Zool. Jahr., Anat., 17: 684—New Hebrides (doubtful).

*Aneitea (Triboniophorus) graeffei* Humbert var. *insularis* Grimpe and Hoffmann, 1925, Nova Caledonia, 3, (10), pp. 442, 448—based entirely on the paper of Glamann (1903).

*Aneitea (Triboniophorus) graeffei* var. *papuensis* van Benthem Jutting, 1933, Nova Guinea, Zool., 17: 90–92—Dutch New Guinea.

*Range*.—New Guinea to southern New South Wales. Possibly introduced into the New Hebrides.

*Material*.—No material available.

*Remarks*.—There are no characters given in Glamann's study by which the "New Hebridean" specimen could be separated from the east Australian forms studied by others. Grimpe and Hoffmann's var. *insularis* was based solely on the locality and need not be carried in the literature. If the New Hebridean locality record is correct, specimens probably were accidentally introduced from Queensland.

### Genus ANEITEA Gray, 1860

Mantle clearly outlined by deep furrows. Shell composed of a single piece. Radula with rudimentary or no central tooth, lateral teeth with four cusps. Oviducal accessory gland far removed from hermaphroditic duct. Kidney with four- to seven-looped ureter. (Modified from Grimpe and Hoffmann, 1925a.)

*Type species*.—*Aneitea macdonaldi* Gray.

*Remarks*.—Grimpe and Hoffmann (1925a) recognized sixteen species and varieties of *Aneitea*: eleven from New Caledonia, four from the New Hebrides, and one from Brisbane, Australia. Hoffmann (1929b) described a fifth species from the New Hebrides. The Brisbane *A. brisbanensis* W. Pfeiffer (1900) was probably introduced into the botanical gardens. The source of the introduced

specimens is unknown. Franc (1957, pp. 97-101) added no new data, but provided a convenient summarization of Grimpe and Hoffmann's studies on the New Caledonian *Aneitea*. The information on morphologic variation presented below raises doubts as to the validity of the many New Caledonian "species," and field studies are needed to clarify the status of the named forms.

The primary character utilized for recognition of species in *Aneitea* has been the shape of the central tooth of the radula. Each specimen examined in this study had a differently constructed central tooth and van Benthem Jutting (1933, p. 90) found similar variability in the New Guinea *Triboniophorus*. Within a species, the central tooth is roughly comparable, but the individual variations exceed the limits of "specific" difference established by Grimpe and Hoffmann (1925a). The central tooth is in the process of being lost and it is a basic tenet of evolutionary theory that vestigial structures are not subject to selection and thus are apt to vary widely. The internal shell of *Aneitea* is deeply grooved and pitted and varies widely in shape. The drawings in Grimpe and Hoffmann (1925a) suggest that the shell provides a guide to recognition of species through its shape, but this is not borne out by the material examined. Color variation in slugs is equally unreliable as a specific character, particularly in preserved specimens. Whether the color pattern in slugs is essentially cryptic (Scharff) or is correlated with temperature (Simroth) is unknown. The New Hebridean slugs show quite different color patterns and there are excellent opportunities for field studies on this factor.

Specimens of the genotype, *A. macdonaldi*, and a series from Espiritu Santo were available for this study. The most constant characteristics separating the two populations were the shape of the jaw, the number of lobes in the hermaphroditic gland, the position of the oviducal accessory gland, the presence or absence of an epiphallic caecum, and the shape of the spermatheca. Without re-examining their original material, it is impossible to evaluate the many species proposed by Grimpe and Hoffmann (1925a). The characters listed above may provide a basis for specific recognition, but more material must be examined before their importance can be evaluated. For convenience the "species" of Grimpe and Hoffmann are briefly discussed below and the original figures of the anatomy reproduced (pl. 3, figs. 5-13).

Slugs collected on Aneiteum, Tanna, and Erromanga are referred to *A. macdonaldi*. The material from Espiritu Santo is most similar to *A. robsoni* Hoffmann but differs enough to be given nomenclatural

recognition. *A. robsoni* was collected on Mount Tabwemasana (6,000 feet), while *A. r. santoensis* came from near the seacoast. The new "subspecies" may only represent a local population, but its true status can only be evaluated when more adequate collections have been made on the island. Grimpe and Hoffmann (1925a) mention that slugs were seen on Ambrym by Speiser but none were collected.

***Aneitea maloensis* Grimpe and Hoffmann.** Plate 3, figs. 5, 9, 11, *a*, 12, *a*.

*Aneitea macdonaldi maloensis* Grimpe and Hoffmann, 1925, Nova Caledonia, 3, (10), pp. 436-438, figs. 15*h*, 16*m*, 17*l* (not *m*), 18*l*, 19*a*, 20; pl. 5, fig. 8*a*, *b*—Malo Island, New Hebrides.

*Range*.—Malo Island.

*Material*.—No material available.

*Remarks*.—Basal plate of rachidian tooth not bifid; tooth itself indistinctly bicuspid. Both upper and basal plate of jaw very wide. Jaw without median projection. Hermaphroditic gland bilobed, epiphallic flagellum lacking. Animal light-colored with two longitudinal black stripes. Shell short and broad.

The differences found in the anatomy of *A. macdonaldi* justify raising this "subspecies" to "specific" rank.

***Aneitea speiseri* Grimpe and Hoffmann.** Plate 3, figs. 6, 10, 11, *b*, 12, *b*.

*Aneitea speiseri* Grimpe and Hoffmann, 1925, Nova Caledonia, 3, (10), pp. 433-436, figs. 15*f*, 16*k*, 17*m* (not *l*), 18*k*, 20, pl. 5, figs. 10*a*, *b*, 11, 12—Espiritu Santo, Malo; Hoffmann, 1929, Zool. Anz., 84, (5-6), pp. 108-109—east central Espiritu Santo.

*Range*.—Espiritu Santo, Malo.

*Material*.—No material available.

*Remarks*.—Rachidian tooth without cusps, only a small basal plate. Basal plate of jaw as in *maloensis*, but upper plate narrower and with low median cutting edge. Hermaphroditic gland bilobed, epiphallic flagellum lacking. Animal darker than *maloensis*, with two or three longitudinal black stripes, or the surface densely spotted with black. Shell elongate, narrow.

***Aneitea elisabethae* Grimpe and Hoffmann.** Plate 3, figs. 7, 8, 11, *c*, 12, *c*.

*Aneitea elisabethae* Grimpe and Hoffmann, 1925, Nova Caledonia, 3, (10), pp. 431-433, figs. 15*g*, 16*l*, 17*k*, 18*i*, 20, pl. 5, fig. 13—Malo; Hoffmann, 1929, Zool. Anz., 84, (5-6), pp. 109-111—Espiritu Santo(?).



*Range*.—Malo and Espiritu Santo(?).

*Material*.—No material available.

*Remarks*.—Central tooth weakly or not bifid, cusps little or not developed. Basal plate of jaw more elongate than in first two species, upper plate narrow, long, with low median projection. Hermaphroditic gland bilobed, epiphallic flagellum lacking. Animal dark in color with rounded posterior. Shell elongate, slightly notched at one end.

The specimens reported by Hoffmann (1929b) differed slightly from the original description, but probably are this "species."

***Aneitea robsoni robsoni* Hoffmann. Plate 3, fig. 13.**

*Aneitea robsoni* Hoffmann, 1929, Zool. Anz., 84, (5-6), pp. 111-114, figs. 3-6—  
Mount Tabwemasana (ca. 6,000 feet), central Espiritu Santo.

*Range*.—Mount Tabwemasana, Espiritu Santo.

*Material*.—No material available.

*Remarks*.—Basal plate of rachidian tooth deeply bifid, cusp structure well developed, distinctly bicuspid. Upper plate of jaw narrow, with prominent median projection, lower plate wide, tapering posteriorly. Hermaphroditic gland trilobed in drawing, bilobed in text. Epiphallus with small caecum(?). Penis strongly coiled. Animal almost black, mantle grooves colorless. Shell elongate, strongly curved.

The dark color of *A. r. robsoni* probably is correlated with its montane habitat and contrasts with the lighter coloration of *A. r. santoensis*. The two subspecies(?) have quite different radulae, jaws, and genitalia, but *santoensis* had best be considered a subspecies until spatially intermediate populations have been sampled.

***Aneitea robsoni santoensis*, new subspecies. Plate 4, figs. 3, 4, 6, 8, 10, 11; plate 13, fig. 1.**

An *Aneitea* similar to *robsoni* in rachidian tooth structure, trilobed hermaphroditic gland, highly convoluted penis, shell, and basic color pattern. It differs from *robsoni* in jaw structure, lack of an epiphallic flagellum, in having the oviducal accessory gland much nearer the albumen gland, and in having only partially pigmented mantle grooves.

Animal (pl. 13, fig. 1) elongate, tapering posteriorly, 22-43 mm. in length (preserved). Color reddish olive green, mottled with black spots on dorsal area. Sole of foot same color as dorsal region, but with fewer black spots. Cephalic

shield triangular, outlined with dark streaks, inner edge of mantle grooves black. Respiratory, anal, and excretory pores nearest lower corner of mantle, distinctly separated and connected only by a groove in the epithelium. Upper plate of jaw (pl. 4, fig. 4) widest at center, tapering distally, without median projection. Basal plate short, broad, not tapering posteriorly. Internal shell (pl. 4, figs. 6, 10) irregular, more deeply grooved and less solid than in *A. macdonaldi*. Radula with 127-135 rows and 115-121 teeth per half row. First few lateral teeth (pl. 4, fig. 11, right) large with well-developed cusps; after nineteenth lateral, the teeth diminish greatly in size. Central tooth varying both in depth and width of bifid basal plate; cusps may be absent (figs. 8, *b-c*) or claw-shaped (fig. 11, left). Genitalia (pl. 4, fig. 3) with trilobed hermaphroditic gland. Ovoid albumen gland with ducts of oviduct and vas deferens issuing near insertion of hermaphroditic duct. Prostate and vas deferens loosely bound to oviduct by connective tissue. End of prostate near oviducal diverticulum. Vas deferens passing along convoluted oviduct to genital atrium, then alongside penis to insertion of penial retractor. Penial retractor arising from body wall on left side, slightly above sole and 5 mm. behind posterior edge of mantle shield. Penis greatly convoluted. No epiphallic caecum. Epiphallus (above lowest convolution) internally sculptured with pustulose nodules; penis proper (below convolutions) with smooth tubercles only. Right ocular retractor passing between male and female genitalia. Spermatheca spherical even when filled with sperm.

*Type*.—American Museum of Natural History. Collected on the leaves of plants and trees near Second Channel, Espiritu Santo, by G. S. Banner on September 9, 1943.

*Paratypes*.—Collected with the holotype and in the collection of the American Museum.

*Remarks*.—The availability of 36 specimens from a single population made possible a study of variation in characters previously used for specific delineation. The shell and rachidian tooth varied extensively and are quite unreliable for identification. In contrast the shape of the jaw seemed constant, as also were the structures and relative proportions of the genitalia. The presence or absence of an epiphallic caecum, the position of the oviducal accessory gland and the shape of the albumen gland seem to be useful in classification. The other "species" from Espiritu Santo need to be re-examined before these criteria can be employed, however.

The penis showed a peculiar dimorphism which is, at present, inexplicable. Most penes were of normal shape, with the penial retractor inserting at the juncture of the "thin" (epiphallic) and the "thick" (penis) sections of the penial complex. In about one-fourth of the animals dissected the upper half of the "thick" section was no larger than the vas deferens. All the parts of the genitalia were normal in proportion so that there was no question of misplacement of the muscle insertion. When first observed it was assumed that

the specimen was immature, but when this condition was found in a mating specimen that possibility was discarded. Both members of the other mating pairs were normal so that the probability of protogyny is lessened.

The bionomics of *Aneitea* are unknown, although it is assumed that the slugs feed on plants. Among the 36 specimens, three pairs were in copulation and two others seemed to have been separated in the preservative. One of the copulating pairs was dissected completely; in the others the apical portions of the penes were examined. Copulation (pl. 13, fig. 1) is head-on and reciprocal. Both penes were inserted into the vaginae and extended about two millimeters beyond the openings to the spermathecae. As is usual in the Stylommato-phora, the penes were everted. In both cases the spermathecae were tightly packed with sperm, a conclusive indication that insemination was mutual. The tubercles of the penes were prominent and evidently served as stimulators. The epiphallus and penial retractor were uncoiled and extended. No traces of a solid spermatophore could be found. The date of collection established that mating occurred in September.

The relationship of *santoensis* to typical *robsoni* is uncertain. The trilobed hermaphroditic gland and the bifid basal plate of the rachidian tooth indicate affinities, but the structure of the jaws is quite different and *robsoni* seems to have a small epiphallic caecum which is lacking in *santoensis*. The latter may prove to be a distinct species, but until the former can be restudied and spatially intermediate populations examined, it is perhaps best to treat it as a subspecies.

***Aneitea macdonaldi* Gray.** Plate 4, figs. 1, 2, 5, 7, 9, 12; plate 13, fig. 2.

"Bitentaculate slug," MacDonald, 1856, Ann. Mag. Nat. Hist., (2), 18: 38-42, pl. 3—*Aneiteum*.

*Aneitea macdonaldi* Gray, 1860, Ann. Mag. Nat. Hist., (3), 6: 195-196.

*Range*.—*Aneiteum*, Tanna, Erromanga.

*Material*.—*Aneiteum* (AMNH, Macmillan, August, 1937); Erromanga (AMNH, Macmillan, March-April, 1937); White Sands, Tanna (AMNH, Macmillan, December, 1936).

*Remarks*.—*Aneitea macdonaldi* has not been reported in the literature since its original collection and description. Hoffmann (1929b) mentioned deficiencies in the original study but they were only the result of the lack of knowledge of molluscan anatomy at that time.

The genitalia, radula, and jaw have been refigured at this time for comparison with *A. robsoni santoensis*.

The animals (pl. 13, fig. 2) range from 22 to 65 mm. in length, with only slight traces of dark mottling and a few dark streaks outlining the cephalic shield. Externally they do not differ from *A. r. santoensis*, and the internal morphology does not differ greatly from that of *A. brisbanensis* (W. Pfeiffer, 1900). The jaw is quite narrow centrally, with a small but distinct median projection. Distally it widens, reaching a maximum width just before the "flaps" bend under. The basal plate of the jaw is only slightly broader than wide. The radula has 118-134 rows with 150+ teeth per row. The lateral teeth of the radula (pl. 4, fig. 5, *b-f*) show the same trends seen in *A. r. santoensis* and the central tooth (pl. 4, fig. 5, *a*) is even more variable than in the latter species. The cusps of *macdonaldi* are more blunted than those of *A. r. santoensis*, a condition possibly caused by feeding on harder substances than its northern relatives do. The shell is narrower than that of most *Aneitea*, varying in outline from elongate-ovate to a rough parallelogram; it is also thicker and more solid than that of *A. r. santoensis*. The genitalia (pl. 4, fig. 1) have the hermaphroditic gland weakly trilobed, with the separate ducts very short and the lobes closely bound; a casual inspection might suggest it is unilobed. The presence of an epiphallic caecum, an elongate spermatheca and the relative position of the oviducal accessory gland are the main characters separating *macdonaldi* from *santoensis*.

Most specimens of *macdonaldi* were juvenile, but four adults were dissected. No significant differences were found between specimens from Tanna, Aneiteum, and Erromanga.

### Order HETERURETHRA Pilsbry, 1900

Jaw elasmognathous. Kidney broader than long, extending from pericardium to hindgut, ureter lying along front margin, then following rectum to pneumostome. Lung short, but with normal venation. Shell oval, thin, with spire of few whorls or uncoiled. (After Pilsbry, 1948, p. 771.)

As utilized in this study, the Heterurethra contains only the family Succineidae. Possibly the African Aillyidae and the Tracheopulmonata may prove to be closely related to the Succineidae (see p. 33).

### Family SUCCINEIDAE

The amber snails are worldwide in distribution and the rudimentary shells provide few characters of value in classification. In recent

years Quick (1933, 1934, 1936, 1939a, b), Boettger (1939), Pilsbry (1948), and Odhner (1950) have attempted to base succineid classification on the structures of the soft parts. Following Odhner (1950), I have placed species without a penial sheath in a subfamily Catellinae, species with a sheath in the Succineinae. Lee (1951) erected a third subfamily in an unpublished thesis, but his action does not affect the status of any of the species considered below. Hawaiian and some Polynesian succineids belong to the Catellinae, but all the Australian, Indonesian, and Melanesian species, as far as now known, belong to the Succineinae.

### Subfamily SUCCINEINAE

A large number of nomenclatural genera are available for the members of this subfamily, but too little is known about individual anatomical variation and too many species have not yet been dissected to enable recognition of many biological groups. Separation of the species with a penial appendix as *Oxyloma* seems justifiable, but it is not possible to go further at the present time.

Genus SUCCINEA Draparnaud, 1801

*Type species.*—*Helix putris* Linnaeus.

*Remarks.*—Many sections of *Succinea*, such as *Novisuccinea* Pilsbry (1948, p. 801) and *Desmosuccinea* Webb (1954, p. 10), have been based on the degree to which the epiphallus and penis are free from the sheath. The variation observed in the specimens studied raises doubt as to the validity of this character for specific, much less generic determinations. Webb (1953, p. 216) has shown that during copulation the "free loop" of the penis and/or epiphallus disappears into the sheath upon extrusion of the penis. This fact provides a ready explanation for variation in the size and prominence of the loop. The differences may be caused by incomplete retraction of the penis after copulation or spasmodic muscular contractions in the killing solution. Apparently a more reliable specific character is the exact point of insertion of the penial retractor muscle on the sheath, penis and/or epiphallus (Pilsbry, 1948, p. 801). Unfortunately this information is known for only a few species. Preserved material of two species, *S. simplex* and *S. kuntziana*, was available to me, and the anatomy of several other Indo-Pacific succineids has been partially figured in the literature.

A survey of published records and two collections of shells (UMMZ and CNHM) indicated that the Austromalayan succineid fauna contains two groups, distinguished by the presence or absence of microscopic criss-cross sculpture on the shell and the relative lengths of radular cusps and basal plates. A group with microscopic criss-cross sculpture and the cusps on the rachidian tooth as long as the basal plate was defined by Quick (1939a, b, 1951). He listed several species probably belonging to it. A later paper by van Benthem Jutting (1952) enabled me to add the Javanese forms. A species described by Abbott (1950), although aberrant in several aspects, probably can be included in the same taxon. The following seem to be related: *obesa* von Martens (Java), *minuta* von Martens (Java), *keelingensis* Abbott (Cocos-Keeling Atoll), *solitaria* Smith (Christmas Island), *australis* Ferussac (Victoria), *norfolkensis* Sykes (Norfolk Island), *caduca* Mighels (Hawaii), *texta* Odhner (Masatierra), *andecola* Crawford (Peru) and *striata* Krauss (South Africa). The sectional name *Austrosuccinea* Iredale (1937a, p. 307, type *S. australis* Ferussac) can be applied to this group. The more recent "genus" *Spirancinea* Iredale (1945, p. 53, type *S. norfolkensis* Sykes) is a probable synonym, although the sculpture of *S. norfolkensis* is much heavier than in the other species examined. The nearly world-wide distribution of succineid genera and sections is well established, although its cause is unknown. Transport of *Succinea* by birds has been reported (see Nautilus, 27, p. 71; 50, p. 31), but the importance of such factors in molluscan distribution can easily be over-emphasized.

A second group of species without any trace of the microscopic sculpture, even under 100× magnification, and with the rachidian cusps much shorter than the basal plates contains the following species: *strubelli* Strubell (Papua), *papuana* Strubell (Papua), *britanniae* Mousson (Bismarek and Admiralty Islands), *simplex* Pfeiffer (Solomon Islands), *kuntziana*, new sp. (New Hebrides), *modesta* Gould (Samoa and Tonga), *archeyi* Powell (New Zealand) and probably the New Caledonian species. The name *Papusuccinea* Iredale (1941, p. 63) is available and has been adopted as a sectional name for these species. Quick (1951) studied the anatomy of *archeyi* and called it an *Austrosuccinea*. The radula with short-cusped rachidian tooth (Powell, 1950) and the lack of criss-cross sculpture on the shell (Quick, 1951) indicate that it is a *Papusuccinea*, a group of species evidently not examined by Quick. Apparently there are no readily discernible differences in the genitalia of *Austrosuccinea* and *Papusuccinea*.

## Section PAPUSUCCINEA Iredale, 1941

Shell smooth, without microscopic criss-cross striations. Radula with mesocone of central tooth extending only slightly past mid-point of basal plate; in *Austrosuccinea* it is at least two-thirds the length of and often as long as the basal plate. Genitalia similar to those of *Succinea avara* of eastern North America, but shell and radula quite different. Penis more slender and vagina longer than in *Calcsuccinea*.

*Type species*.—*Succinea strubelli* Strubell.

*Remarks*.—Members of *Papusuccinea* replace each other geographically in a long arc from New Guinea to New Caledonia (see Franc, 1957, pp. 94–96, for New Caledonian *Succinea*). There is a species in Samoa and Tonga, but no succineids have been reported from the Fijis. Conchologically the species are very similar and records in the literature are quite untrustworthy for specific designations. I. Rensch (1937, p. 593) suggested they may represent a classical Rassenkreis. Pending anatomical studies of the entire complex, however, it is perhaps best to consider them distinct species. Previously published figures of the genitalia of species of *Papusuccinea* do not illustrate diagnostic characters, nor do accounts of the radula offer sufficient information to enable proper allocation of the nomenclatural units listed above. It is not possible to determine the affinities of *Austrosuccinea* and *Papusuccinea* to “genera” found in other areas.

The New Hebridean succineid has been recorded in the literature, but not named. I take great pleasure in naming it after Commander Robert E. Kuntz, whose donation of so much carefully preserved and localized material made this study possible.

***Succinea (Papusuccinea) kuntziana***, new species. Plate 5, figs. 1, 3–8; plate 13, fig. 3.

*Succinea* sp. Sykes, 1903, Proc. Malac. Soc. London, 5: 198—Valua, Banks Islands and Vila, Vate.

*Succinea simplex* Iredale (not Pfeiffer, 1855), 1941, Australian Zool., 10, (1), p. 63—New Hebrides.

A *Papusuccinea* with flatter whorls and fewer lateral teeth than are found in *S. simplex* Pfeiffer from the Solomon Islands, and with smaller nuclear whorls and less elongate spire than *S. montrouzieri* Crosse from New Caledonia.

Shell thin, elongate-ovate, translucent, light horn-colored, apex often reddish. Whorls  $2\frac{1}{2}$  to 3, gently rounded. Spire-aperture ratio 0.27 to 0.40 in adults; young shells with a lower ratio and whorls more sharply rounded than in adult. Surface uneven and slightly pitted. Growth striae absent to prominent. Radula

with 78 to 112 rows, formula (13-20)-(7-9)-1-(7-9)-(13-20). Mesocone of central tooth (pl. 5, fig. 3, *a*) slightly less than two-thirds the length of basal plate. Lateral and marginal teeth (pl. 5, fig. 3, *b-d*) with small endocone, occasionally lacking. Jaw (pl. 5, fig. 6) without accessory ribs and having only a small median projection. Talon (pl. 5, figs. 1, 5) unequally bilobed in many specimens. "Free loop" of epiphallus (pl. 5, fig. 8) completely contained within the penial sheath in a few specimens (pl. 5, figs. 1, 7), partially protruding in the majority. Penis slender. Penial retractor inserting at junction of epiphallus and vas deferens, some fibers attaching to penial sheath. Penis and epiphallus undifferentiated externally except for a slight constriction at their junction, concealed by the penial sheath. Epiphallus sculptured internally by a series of longitudinal beaded ridges. Penis with four to six unbeaded longitudinal ridges. The same pattern is found in the North American *Succinea avara* (Pilsbry, 1948, p. 818, fig. *b*). Height of shell 8.2 to 12.8 mm., diameter 5.4 to 8.0 mm., height of aperture 5.4 to 8.0 mm.

*Type*.—University of Michigan Museum of Zoology no. 183566. Collected at Mlle. Havet Plantation on Espiritu Santo (ML 96) by Robert E. Kuntz in July, 1944.

*Paratypes*.—On Espiritu Santo, Kuntz collected specimens at the following stations: ML 13, ML 22, ML 26c, ML 31f, ML 39, ML 43, ML 46, ML 63, ML 64, ML 69, ML 70, ML 74, ML 76a, ML 96 (type locality). Most of these are in the University of Michigan Museum of Zoology. Some have been distributed to other institutions (CNHM, MCZ, ANSP, BPBM, USNM, and Australian Museum, Sydney). Other paratypic material includes: USNM 432456 (Espiritu Santo); USNM 515359 (Tanna); and USNM 598358 (Vila, Vate, ex Miller 452).

*Range*.—Espiritu Santo, Valua (Banks Group), Vate, and Tanna. It probably will be found on most of the other islands.

*Remarks*.—Through the kindness of Dr. William J. Clench, one adult and one juvenile specimen of *Succinea simplex* Pfeiffer from Paivi, Ugi, Solomon Islands, were made available for dissection. Unfortunately the specimens had previously been preserved in formaldehyde. The radulae and jaws were extracted and the general facies of the male genitalia could be observed, but the hardness of the tissues made critical studies impossible. The radular teeth are quite similar to those of *kuntziana*, although the mesoconal cusp of the central tooth is slightly shorter in *simplex*, and the endocone of the lateral teeth is more developed in the latter species. There may be a clinal gradient in the endoconal development of the lateral teeth in *Papusuccinea*. The endocone is very much reduced in *S. kuntziana*, stronger in *S. simplex* and quite prominent in *S. brittaniae* Mousson (I. Rensch, 1937, p. 593, fig. 38). *S. kuntziana* and *S. simplex* differ in radular formula. The adult of the latter has the formula 15-13-1-13-15, and the juvenile (4.2 mm. high) has the formula 15-



9-1-9-15. Quick (1934) correlated changes in radular formula with increase in shell size in two British species. His data show that even in specimens three and four millimeters in height, differences in the number of lateral teeth are significant. A 4 mm. specimen of *kuntziana* had only five lateral teeth. In view of the results of Quick's study the difference between *S. simplex* and *S. kuntziana* is considered to be of specific value. *S. strubelli* (see Hedley, 1892b, p. 691) has the formula 16-13-1-13-16; I. Rensch (1937, p. 593) has reported 51-53 teeth "in einer halben Reihe" of *S. brittaniae* without giving the actual formula, but no other *Papusuccinea* have been examined. No significant differences were found in the genitalia of *S. kuntziana* (pl. 5, fig. 1) and *S. simplex* (pl. 5, fig. 9). The anatomical figures of succineids given by B. Rensch (1932, p. 127, figs. 52, 55) and I. Rensch (1937, p. 593, fig. 37) do not treat diagnostic characters. Seemingly, as in all succineids, the jaws of the sections *Austrosuccinea* and *Papusuccinea* show no constant differences.

Specimens of *S. modesta* from Tutuila, Samoa, have a more obese shell. No authentic material of succineids from the Bismarcks or New Guinea was available. Adult *simplex* and *kuntziana* are illustrated (pl. 13, figs. 3-4). The juvenile shells of *S. kuntziana* are nearly as rounded as those of *S. simplex*. The characteristic flatness of the whorls of *S. kuntziana* is apparent only in specimens with  $2\frac{3}{4}$  or more whorls. Material from Tanna and Vate (USNM) is juvenile, with only  $2\frac{5}{8}$  whorls. One adult shell from Miller (number 542) showed no differences from the Espiritu Santo adults.

*S. kuntziana* was collected on Espiritu Santo from October, 1943, to June, 1944, but no definite reproductive pattern was discernible. Young shells (less than 5 mm. in height) were found in October and May, half-grown specimens (5-7 mm.) in October, January and June, and adults (more than 7 mm.) in December, January, April and June. Powell (1950) reported an annual life cycle for the New Zealand succineid; a similar cycle has been established for several North American species, but the data on *S. kuntziana* are insufficient to establish its life span.

Most living specimens of *S. kuntziana* were collected under piles of decaying leaves, sticks, or palm fronds in heavy shade. Many were found in areas near streams, but one lot (ML 39) was found on a hillside and a few adults were collected on the trunks of trees and shrubs during a rain (ML 31f). Except for *S. archeyi* (Powell) (1950), all *Papusuccinea* have similar ecology. Both *S. simplex* Pfeiffer (see E. A. Smith, 1885) and *S. strubelli* (see Hedley, 1892b) live in native

gardens near water. The general habitat of *Papusuccinea* is similar to that of the North American *avara* complex, which seems to be a group convergent, if not related, to *Papusuccinea*.

### Order ORTHURETHRA Pilsbry, 1900

Holopod snails with the kidney tapering anteriorly into the ureter, which runs directly forward, remote from the hindgut and opens within the forward border of the lung. (After Pilsbry, 1948, p. 848.)

Division of the Orthurethra into family categories is still provisional. Watson (1920) recognized four families, Steenberg (1925) sixteen, and H. B. Baker (1956a) ten. Pilsbry (1948, p. 848) considered that families are primarily recognized on the basis of expediency and that shell characters are often more useful in classification of the Orthurethra than the soft parts. This apparent similarity in anatomy may be more the result of convergent evolution than any basic conservatism, but much work needs to be done before a definitive classification can be attempted. Of the ten families recognized by H. B. Baker (1956a), four—Pupillidae, Enidae, Tornatellinidae, and Partulidae—are found in the New Hebrides. The single enid is very probably introduced. The single pupillid and two tornatellinids are found over much of the Pacific and probably have been dispersed by natives. Only the partulids form an important endemic part of the fauna.

### Family PUPILLIDAE (=Vertiginidae)

Genera such as *Nesopupa*, *Pupisoma*, and *Cylindrovertilla* may subsequently be found in the New Hebrides, but only the very wide-ranging *Gastrocopta pediculus* (Shuttleworth) is known from the islands at the present time.

### *Gastrocopta (Sinalbinula) pediculus* (Shuttleworth)

*Pupa pediculus* Shuttleworth, 1852, Mitth. Naturf. Gesell. Bern, 1852: 296—Marquesas Islands.

*Gastrocopta pediculus* (Shuttleworth) Pilsbry, 1917, Man. Conch., (2), 24: 145—152, pl. 25, figs. 1–3, 5–8, 12–15.

*Range*.—Espiritu Santo. From Java to Australia, New Caledonia, all of Polynesia and Micronesia and Hawaii.

*Material*.—ML 35, ML 39, ML 40, ML 69, ML 78, ML 95.

*Remarks*.—The range of *Gastrocopta pediculus* and its occurrence only at lower elevations on high islands (Pilsbry, 1917, p. 148) lends

credence to the possibility that it may have been introduced over much of its range. Several weakly characterized varieties have been named. Although a few New Hebridean specimens may qualify as these forms, the great majority were typical *pediculus*.

### Family ENIDAE (= **Buliminidae**)

Enids are common in the temperate and tropical regions of Africa, Europe, and Asia. The distribution and taxonomy of the African and European species have been extensively studied, although serious gaps in our knowledge still remain. The exact limits of distribution in Asia are very uncertain. Enids are common in India and China, and members of the typical subfamily, Eninae, are reported from Java (van Benthem Jutting, 1952, pp. 366-373) and Lombok (B. Rensch, 1932, pp. 118-119). Another series of species close to, if not congeneric with, the South African *Rhachistia*, is discussed below.

The status of several fringe groups is less certain. *Pseudonapaeus apertus* (Martens), found on Timor (B. Rensch, 1935, p. 320), has typically enid radular dentition but the genital anatomy is unknown. *Apoëcus colonus* (Milf.) from Constantinhaven, New Guinea (see Kobelt, 1902a), although unknown anatomically, is similar enough to *Pseudonapaeus apertus* to be tentatively referred to the Enidae (see Solem, in press-B). *Aminopina* Iredale (1933, p. 42; 1938, p. 93; 1941, p. 64) from New Guinea and northern Queensland probably is an enid (see Solem, op. cit.).

Thus, enids are known definitely from Java, Lombok and Timor, and possibly from Australia and New Guinea (fig. 16). No species referable to the Enidae have been reported from the Bismarcks, the Solomon Islands, New Zealand or Polynesia. Many enids are conchologically similar to the Partulidae, which possibly will be found to be ancestral to the Enidae. In the Partulidae there are no accessory organs on the penis; accessory organs are always present in the Enidae. In this respect the enid-partulid may parallel the helicid-camaenid relationship in the holopod Sigmurethra.

Subfamily relationships within the Enidae are obscure. The most recent classification is that of Thiele, who places the New Hebridean species in the Pachnodinae. I have accepted his classification but have made no attempt to characterize the subfamily. The Pachnodinae are found chiefly in southern Africa and Asia, although a few species live on the Mediterranean islands. There is a large group of

very similar species found in South Africa, India, southeast Asia, the Philippines, Celebes, Timor, New Hebrides, New Caledonia and Queensland. Thiele (1931) and Connolly (1939) place them in a single genus, *Rhachistia*; Tomlin and Peile (1930) put the Asiatic species in a new genus *Eorrhachis*; and Iredale (1933) created a new genus, *Rachispeculum*, for the Queensland "species." There are only minor conchological differences between African and New Hebridean specimens and radular structure is identical (see Tomlin and Peile, 1930). Study of the genitalia may indicate that *Eorrhachis* is a valid genus, but in the light of our present knowledge only one genus is admissible.

### Genus **RHACHISTIA** Connolly, 1925

(= **Eorrhachis** Tomlin and Peile, 1930, and **Rachispeculum** Iredale, 1933)

Shell comparatively large, short turriform, solid, smooth, fairly glassy, with dark spots and brown or purple bands on ground of rose, buff, flesh, or cream. Aperture ovate, peristome acute, not expanded. Teeth of radula large, lobe-shaped, central single, blunt or round (Connolly, 1939, pp. 418-419).

*Type species.*—*Buliminus rhodotaenius* Martens.

*Remarks.*—The Asiatic species of *Rhachistia* have been characterized mainly on the basis of color pattern. *R. sulphureus* (Tomlin and Peile) has only a few maculations, and *R. zonulatus* (Pfeiffer) has a series of spiral bands and spots. *R. zonulatus* has been reported from Timor, the Celebes, and the Philippines. The spotty distribution of both *zonulatus* and *histrion* suggests that they may be introduced species, since *R. punctatus* Anton is an Indian species widely introduced into Africa (Pilsbry, 1919, pp. 304-315). *R. histrion* is known from Queensland, New Caledonia, and the New Hebrides. A lot labeled Tamatave, Madagascar (CNHM 48032), appears to be typical *histrion* and I suspect that *R. histrion* may prove to be an African species imported to New Caledonia and then to the New Hebrides and Queensland.

### **Rhachistia histrion** (Pfeiffer). Plate 8, fig. 9; plate 13, fig. 5.

*Bulimus histrion* Pfeiffer, 1854, Proc. Zool. Soc. London, 1854: 124—Tanna.

*Bulimus magenii* Gassies, 1856, Jour. de Conch., 5: 181, pl. 6, fig. 5—New Caledonia.

*Bulimus bidwilli* Cox, 1868, Monog. Australian Land Shells, p. 72, pl. 13, fig. 11—Burnett River, Queensland ("in the tops of trees").

*Buliminus (Rhachis) histrion* (Pfeiffer) Kobelt, 1902, Conch. Cab., I, 13, (1), p. 749, pl. 110, figs. 9, 10.

*Buliminus (Rhachis) bidwilli* (Cox) Kobelt, 1902, op. cit., pp. 752-753, pl. 110, figs. 18, 19.

*Rhachis magenii* (Gassies) Sykes, 1903, Proc. Malac. Soc. London, 5: 198—Vila, Vate.

*Rhachistia (Eorrhachis) histrio* (Pfeiffer) Cockerell, 1937, Nautilus, 51, (1), p. 35. Implies that *histrio* might be introduced.

*Rachistia* (sic) (*Eorrhachis*) *histrio* (Pfeiffer) Franc, 1957, Mem. Mus. Nat. d'Hist. Nat., N.S., (A), Zoologie, 13: 108, pl. 11, fig. 141.

*Range*.—Tanna, Vate, Loyalty Islands, New Caledonia, Queensland, and Madagascar(?).

*Material*.—Vila, Vate (USNM 598634, Miller); many lots (UMMZ and MCZ) from New Caledonia, Loyalty Islands, and Queensland. Photograph of holotype of *Bulimus histrio* Pfeiffer (courtesy of BM).

*Remarks*.—The holotype of *Bulimus histrio* Pfeiffer (pl. 8, fig. 9) is juvenile and has a color pattern quite dissimilar to the specimens figured by Kobelt (1902a) as this species. The color pattern in the twenty lots seen varied widely and encompassed the descriptions of *histrio*, *magenii*, and *bidwilli*, as well as the color forms named by Gassies (1871) and Crosse (1894). The color varies from albino to a pattern of four dark color bands and a row of spots. The Vate specimens (pl. 13, fig. 5) lack the two upper color bands and closely resemble the type figure of *magenii*. Numerous New Caledonian specimens are as fully colored as Kobelt's *histrio*; others are albino or had the *magenii* pattern. The size, shape, and sculpture of the holotype and the New Caledonian and New Hebridean specimens are identical. The name *histrio* is retained, despite the wide divergence of the color pattern of the holotype from that shown in Kobelt's figures and the Vate specimens.

The figures, description, and specimens of *bidwilli* leave little doubt that it is the same species as *R. histrio*. *R. bidwilli* has been found in the Port Curtis district, Port Denison, Bundaburg, Mount Dryander, and near Maryborough, Queensland. All are near the active centers for the blackbirding trade between the New Hebrides and Queensland during the late 1800's. There was thus ample opportunity for accidental importation either to or from Queensland. In the majority of cases the occurrence of a snail away from human habitation is an indication that it is "native." From the published records, it is probable that *bidwilli* has been collected "in the scrub" away from the cities, although the recorded localities are all from coastal regions. This is not significant, as *R. punctatus* has become similarly adapted in Africa (Pilsbry, 1919, pp. 304-305). Iredale's

belief that *bidwilli* is a derivative from a *Papuina*-like shell indicates lack of familiarity with non-Australian Mollusca.

### Family TORNATELLINIDAE

A monograph of the Tornatellinidae by the late C. Montague Cooke and Dr. Yoshio Kondo is in press at the Bishop Museum, Honolulu. For this reason, diagnoses of higher taxa and discussions of distribution, phylogeny, and systematics are not given below. The Tornatellinidae are found on most islands of the Indian and Pacific Oceans (fig. 13). A few genera reach the Galapagos and Juan Fernandez Islands but no tornatellinids have been reported from continental areas. The previous major studies on the Tornatellinidae are those of Pilsbry and Cooke (1915-16) and Odhner (1922). I tentatively identified the two New Hebridean species, and then forwarded them to Dr. Kondo at the Bishop Museum. I am indebted to Dr. Kondo for his kindness in checking my identifications and for providing me with the information of the distribution of the Tornatellinidae included in my zoogeographic survey.

Genus **ELASMIAS** Pilsbry, 1910

**Elasmias apertum** (Pease)

*Range*.—Espiritu Santo. Widely distributed in Polynesia.

*Material*.—ML 95.

*Remarks*.—The New Hebridean specimens of *E. apertum* are most similar to the Huaheine, Society Island, shell figured by Pilsbry and Cooke (1915-16, pl. 30, fig. 3). *E. apertum* is extremely widely distributed in the Pacific and is an inhabitant of many coral atolls.

Genus **LAMELLIDEA** Pilsbry, 1910

**Lamellidea pusilla** (Gould)

*Range*.—Espiritu Santo, most of Polynesia, Micronesia, and Melanesia.

*Material*.—Espiritu Santo (USNM 432457; Harrington).

*Remarks*.—The single adult specimen is referred to *L. pusilla* on the authority of Dr. Kondo. Younger specimens of the same species were seen from the Solomon Islands (UMMZ) during this study. *L. pusilla* is easily separated from *Elasmias apertum* by the globose

shape and apertural folds present in the adult of the latter. Young *L. pusilla* have prominent teeth, which are lost in the adult, and are elongate conic in shape.

### Family PARTULIDAE

Pilsbry (1909), Pilsbry and Cooke (1934a, p. 21), and Kondo (1948) emphasize that the Partulidae are related to the Orthurethra rather than the sigmurethrous Bulimulidae as suggested by Thiele (1931, p. 658). Placement of the Partulidae in the Orthurethra is relatively certain, but as yet no pulmonate family can be definitely selected as either its ancestor or its descendant. A few Tertiary fossils have been erroneously referred to *Partula*, but there is no fossil record (Pilsbry, 1909, p. 164).

The Partulidae (fig. 12) are confined to the high islands of the southern and western Pacific. A few species are found in the Palau, Caroline, and Mariana Islands, but the main development occurred in Polynesia and Melanesia(?). The Society Islands, with the largest number of species, have been studied by Crampton (1916, 1932). The partulid fauna of the Marquesas, Australs, Samoan, Fijian, and Tonga Islands is less well known, and *no* speciation studies have been made on the Partulidae of Melanesia or Micronesia (except Guam, by Crampton, 1925). No partulids are known from New Caledonia, Hawaii, the Marshall Islands, or any part of the Indo-Australian archipelago, except eastern New Guinea and the Louisiades.

Pilsbry (1900b, p. 568, and 1909, pp. 166-167) and Crampton (1932, pp. 194-197) cited *Partula* as evidence of a former Pacific continent, but the involved phylogeny and leaf-clinging habit suggest that passive dispersal by winds may have played an important part in their distribution.

Early students of the Partulidae were W. Harper Pease, Andrew Garrett and W. H. Hartman. Their contributions have been summarized by Pilsbry (1909). Subsequent studies on variation by Crampton (1916, 1925, 1932), while not concerned with New Hebridean species, give valuable information as to the extent and trends of variation within the family. For many years the family Partulidae was considered monogeneric, but Pilsbry and Cooke (1934a) recognized several genera and subgenera based on anatomical differences.

Dr. Yoshio Kondo recently completed an extensive anatomical survey of the Partulidae. His conclusions as to generic and anatomical relationships were generously made available to me and are in-

corporated here with his permission. Time and distance have not allowed co-operation on specific relationships and Dr. Kondo is in no way responsible for any errors and omissions in regard to individual species. Of the three genera Kondo recognizes, only one, *Partula*, is found in Melanesia. The Melanesian partulids are all true *Partula* and have one or the other of the two most generalized types of penial structure. These types are found throughout the range of the genus and are of no value in recognition of subgeneric or sectional categories. The Melanesian species are thus placed in *Partula* without subgeneric designations. Kondo (personal communication) informs me that the Melanesian partulids probably represent a backwater of partulid evolution and are neither primitive nor advanced.

The present survey of New Hebridean partulids is based on a re-examination of Hartman's collection (now in CM) and study of specimens in several other museums. In only one case were more than two or three specimens of a species available and no anatomical material was seen. A critical revision could not be attempted, but types have been refigured, errors in localities corrected and the "species" grouped into "superspecies." It is very probable that these "superspecies" are biological species and that the "species" will be recognized as synonyms or local races when adequate series are available for study.

After exclusion of spurious records and species of uncertain status, there are five recognizable groups of partulids in the New Hebrides. *P. vanikorensis*, *P. minor* Hartman and *P. milleri*, new species, are related to Solomon Island species; and there are three "superspecies" seemingly restricted to the New Hebrides.

#### Genus **PARTULA** Ferussac, 1821

On conchological criteria the Melanesian species of *Partula* can be divided into two series, one restricted to the New Hebrides, the other ranging from Espiritu Santo to New Guinea. They differ in size, prominence of spiral sculpture and development of the parietal callus. A complete discussion of their differences is given in Solem (in press-A). *P. minor*, *P. vanikorensis*, and *P. milleri* belong to the second series. The first series contains three "superspecies," grouped around *P. macgillivrayi* Pfeiffer, *P. pyramis* Hartman and *P. auraniana* Hartman. The third group is quite distinct, but the interrelationship of the other two is uncertain. Typically they are easily separable, but a few puzzling lots were seen. Without further mate-



rial it cannot be decided whether the first two "superspecies" represent two taxonomic entities or are a series of convergent intraspecific variations. From notes accompanying the Hartman collection it is evident that Hartman came to believe that the *macgillivrayi* and *pyramis* series were actually only one species. The probability of this is admitted, but without more material than was available the two series should tentatively be considered distinct on the basis of the differences noted below. The morphometry of the New Hebridean partulids is summarized in Table II.

#### SUPERSPECIES OF *Partula macgillivrayi*

Shell slightly smaller than in the *pyramis* group (usually less than 23 mm. high), sculpture lighter, fading out on the last whorl except at the base, sutures less impressed and whorls less rounded. Little or no parietal callus and columellar callus reduced. Color pattern of longitudinal bands and a strong to subobsolete spiral band near the periphery of the body whorl.

The species are quite similar, differing only by minor variations in color, shape and sculpture. There has been much confusion as to relationships, partly because of lack of material and partly because the exact morphotype of each taxonomic unit was uncertain. Figuring of type material fixed the morphotypes, but the question of relationships can only be settled by field studies. Until adequate series from Aneiteum, Erromanga, Tanna and Vate are available, it is probably best to consider the "species" distinct entities.

#### *Partula macgillivrayi* Pfeiffer. Plate 9, fig. 1.

*Partula macgillivrayi* Pfeiffer, 1855, Proc. Zool. Soc. London, 1855: 97—New Hebrides (MacGillivray); Pfeiffer, 1857, Nov. Conch., 1: 61, pl. 17, figs. 14, 15; Pilsbry, 1909, Man. Conch., (2), 20: 278, pl. 33, figs. 15, 16.

*Range*.—Aneiteum.

*Material*.—New Hebrides (UMMZ 145746). Photograph of holotype (BM).

*Remarks*.—The photograph of the holotype (pl. 9, fig. 1) shows that *macgillivrayi* has a wider, more reflexed columella, more truncate base, more prominent sculpture, and slightly more rounded whorls than do other members of the *macgillivrayi* superspecies. There is no suprasutural cord. Cox (1868) reported *P. macgillivrayi* from Aneiteum and the type locality is restricted to that island. From information in Layard's notes, it probably will be found on the southwest part of Aneiteum.

Table II.—Measurements of the New Hebridean Partulidae

| Species                              | Height    | Diameter  | H/D       | Spire    | Aperture  | S/A       | Whorls                           |
|--------------------------------------|-----------|-----------|-----------|----------|-----------|-----------|----------------------------------|
| <i>P. macgillivrayi</i> .....        | 23.5      | 13.0      | 1.81      | 11.4     | 12.1      | 0.94      | 5 $\frac{1}{4}$                  |
| <i>P. turneri</i> .....              | 21.2      | 11.9      | 1.78      | 9.6      | 11.6      | 0.83      | 5 $\frac{1}{2}$                  |
| (elongate).....                      | 22.5      | 12.0      | 1.88      | 10.8     | 11.7      | 0.92      | 5 $\frac{1}{2}$                  |
| <i>P. perstrigata</i> (ANSP).....    | 21.7      | 13.4      | 1.62      | 10.0     | 11.7      | 0.86      | 5 $\frac{3}{8}$                  |
| (AMNH).....                          | 21.7      | 13.5      | 1.61      | 9.7      | 12.0      | 0.81      | 5 $\frac{1}{8}$                  |
| <i>P. caledonica</i> (mean).....     | 21.7      | 11.7      | 1.85      | 10.2     | 11.6      | 0.88      | 5 $\frac{1}{2}$                  |
| (range of 17).....                   | 20.2-23.3 | 11.1-13.0 | 1.77-1.93 | 9.2-11.2 | 10.9-12.6 | 0.82-0.96 | 5 $\frac{1}{4}$ -5 $\frac{5}{8}$ |
| <i>P. pyramis</i> .....              | 24.5      | 13.2      | 1.86      | 11.3     | 13.2      | 0.86      | 5 $\frac{1}{2}$                  |
| .....                                | 23.5      | 13.2      | 1.77      | 11.1     | 12.4      | 0.90      | 5 $\frac{3}{8}$                  |
| <i>P. eximia</i> .....               | 23.2      | 12.0      | 1.93      | 11.6     | 11.6      | 1.00      | 5 $\frac{3}{8}$                  |
| <i>P. albescens</i> (CM).....        | 23.0      | 12.8      | 1.80      | 10.8     | 12.2      | 0.89      | 5 $\frac{1}{2}$                  |
| .....                                | 23.4      | 12.2      | 1.92      | 10.9     | 11.8      | 0.87      | 5 $\frac{1}{2}$                  |
| .....                                | 22.5      | 12.2      | 1.85      | 10.7     | 11.8      | 0.91      | 5 $\frac{1}{2}$                  |
| .....                                | 23.7      | 13.1      | 1.82      | 11.1     | 12.6      | 0.88      | 5 $\frac{5}{8}$                  |
| (mean).....                          | 23.2      | 12.6      | 1.85      | 10.9     | 12.3      | 0.89      | 5 $\frac{1}{2}$                  |
| <i>P. albescens</i>                  |           |           |           |          |           |           |                                  |
| (ANSP 60584).....                    | 21.7      | 12.3      | 1.77      | 10.2     | 11.5      | 0.89      | 5 $\frac{3}{8}$                  |
| (ANSP 144263, mean of 4).....        | 22.8      | 12.2      | 1.87      | 11.3     | 11.5      | 0.98      | 5 $\frac{3}{4}$                  |
| <i>P. aurantiana</i> , holotype..... | 18.6      | 11.2      | 1.66      | 8.3      | 10.3      | 0.81      | 5                                |
| .....                                | 17.7      | 11.2      | 1.58      | 7.6      | 10.1      | 0.75      | 4 $\frac{7}{8}$                  |
| .....                                | 18.4      | 11.2      | 1.64      | 8.0      | 10.4      | 0.77      | 4 $\frac{7}{8}$                  |
| .....                                | 18.1      | 11.1      | 1.63      | 7.6      | 10.5      | 0.72      | 5                                |
| (mean).....                          | 18.2      | 11.2      | 1.63      | 7.8      | 10.3      | 0.76      | 4 $\frac{15}{16}$                |
| (UMMZ 145681).....                   | 17.4      | 10.3      | 1.69      | 7.6      | 9.6       | 0.78      | 4 $\frac{5}{8}$                  |
| <i>P. fraterna</i> , holotype.....   | 20.3      | 12.0      | 1.69      | 9.4      | 10.9      | 0.86      | 5 $\frac{1}{2}$                  |
| <i>P. carnicolor</i> , paratype..... | 21.4      | 11.6      | 1.85      | 10.4     | 11.0      | 0.94      | 5 $\frac{1}{4}$                  |
| holotype.....                        | 23.8      | 12.0      | 1.99      | 12.0     | 11.8      | 1.02      | 5 $\frac{1}{2}$                  |
| <i>P. minor</i> , holotype.....      | 16.4      | 9.0       | 1.82      | 7.5      | 8.9       | 0.84      | 5 $\frac{1}{4}$                  |
| .....                                | 14.4      | 8.5       | 1.70      | 6.2      | 8.2       | 0.76      | 5 $\frac{1}{4}$                  |
| <i>P. milleri</i> , holotype.....    | 15.8      | 9.1       | 1.74      | 7.2      | 8.6       | 0.84      | 4 $\frac{7}{8}$                  |
| <i>P. vanikorensis</i> .....         | 21.1      | 12.2      | 1.73      | 8.7      | 12.4      | 0.70      | 5                                |

**Partula radiosa** (Pfeiffer). Plate 9, fig. 3.

*Bulimus radiosus* Pfeiffer, 1854, Proc. Zool. Soc. London, 1854: 58—New Hebrides.

*Buliminius (Rhachis) radiosus* (Pfeiffer) Kobelt, 1902, Conch. Cab., I, 13, (2), p. 987.

*Range*.—New Hebrides.

*Material*.—Photograph of holotype (BM).

*Remarks*.—The juvenile holotype was the first New Hebridean partulid seen by Pfeiffer. The similarity in sculpture and coloration to many buliminids makes this error in describing it as an enid excusable. It is evident from the photographs that *Partula radiosa* and *macgillivrayi* (pl. 9, fig. 1) are very closely related. The only difference is the presence of a supra-sutural cord in *P. radiosa*. The type locality of *radiosa* is unknown, but it is probably from one of the southern islands.

**Partula turneri** Pfeiffer. Plate 9, fig. 9; plate 16, figs. 2, 3.

*Partula turneri* Pfeiffer, 1860, Proc. Zool. Soc. London, 1860: 40—Erromanga (Turner); Pilsbry, 1909, Man. Conch., (2), 20: 277, pl. 33, figs. 5, 6.

*Partula turneri perstrigata* Pilsbry, 1909, Man. Conch., (2), 20: 277, pl. 33, fig. 4—Tanna.

*Partula (Melanesica) turneri perstrigata* (Pilsbry) Pilsbry and Cooke, 1934, Occ. Pap. B. P. Bishop Mus., 10, (14), p. 15, figs. 5c, d (anatomy)—Tanna (Robertson).

*Range*.—Erromanga, Tanna.

*Material*.—New Hebrides (UMMZ 14035, MCZ 24836, CM 62.4303 ex Geale, CM 62.4304 ex Brot); Tanna (CM 62.4302 ex Geale, ANSP 69174, paratype of *perstrigata*); Erromanga (AMNH, Macmillan). Photograph of syntype (BM).

*Remarks*.—Typical *turneri* is elongate and *perstrigata* is short and obese. Both variations were found in specimens from Tanna and Erromanga, but each lot was assignable to one variety or the other. No mixed lots were seen. The syntype of *P. turneri* (pl. 9, fig. 9), however, is intermediate between the elongate and the obese series and the separation based on material in American museums cannot be maintained. *P. turneri* has no supra-sutural cord and the markings are much lighter than those of *P. macgillivrayi*. The type locality is uncertain. The original specimens of *P. turneri* were obtained from the Rev. George Turner. It could not be ascertained if Turner actually visited Erromanga, but the specimens might have been collected by Samoan missionary teachers.

**Partula caledonica** Pfeiffer. Plate 9, fig. 2; plate 14, figs. 1-4.

*Partula caledonica* Pfeiffer, 1861, Proc. Zool. Soc. London, 1861: 389—New Caledonia (error); Brazier, 1871, Proc. Zool. Soc. London, 1871: 585—correction of type locality to Havannah Harbour, Vate, and report of it from Vanua Lava, Banks Group; Pilsbry, 1909, Man. Conch., (2), 20: 278-279, pl. 33, figs. 12-14.

*Partula pfeifferi* Crosse, 1871, Jour. de Conchy., 19: 184—substitute name.

*Range*.—Vate.

*Material*.—Vate (CM 62.4287, ex Brazier), Havannah Harbor, Vate (CM 62.4286, CM 62.4288), Vila, Vate (ANSP 133297, ex Froggatt; USNM 598361 and Miller 542, coll. by W. B. Miller).

*Remarks*.—*P. caledonica* is the only New Hebridean partulid of which series of shells were available. Two lots were from near Vila; Froggatt's shells were of uncertain locality and Miller's came from the banks of a small stream about two miles north of Vila. Two lots were from the type locality, Havannah Harbor (CM 62.4286, CM 62.4288, collected by Brazier in 1865). All the specimens corresponded well to the syntype (pl. 9, fig. 2). Four of the ten specimens collected by Miller are illustrated (pl. 14, figs. 1-4) to show the infra-populational variation in shell contour and apertural shape. One specimen of *P. caledonica* from near Vila (pl. 14, fig. 4) is similar to *P. pyramis*, but the sutures are less deeply impressed. The only character separating *P. caledonica* from *P. turneri* is the development of a subsutural cord and darker coloration in *P. caledonica*. Brazier's (1871, p. 585) report of *P. caledonica* from Vanua Lava needs confirmation. Hartman (1886, p. 34) described *P. proxima* from specimens collected on Vanua Lava by Brazier, and the record of *P. caledonica* is probably based on the same specimens.

#### SUPERSPECIES OF *Partula pyramis*

Shell larger than in the *macgillivrayi* series (usually more than 23 mm. high). Sculpture more prominent, continuing over the last whorl. Suture well impressed and whorls strongly rounded. Parietal and columellar calluses well developed. The coloration is unknown, as most individuals seen have been quite worn.

Sykes (1903, p. 198) first postulated the unity of these species and study of type specimens and photographs confirms his conclusion. The *pyramis* complex has a slightly more elongate shell with more impressed sutures than the *macgillivrayi* series. The differences are more of degree than sharp separation and the two groups may be ecological variations, rather than distinct taxonomic entities. The worn condition of the specimens of the *pyramis* "superspecies"

may indicate that they have been washed down from higher elevations and collected from stream drift. The elongate spire and impressed sutures could then be correlated with the same type of variation found in *Diplomorpha* (see pp. 139–141).

### **Partula pyramis** Hartman. Plate 14, fig. 9.

*Partula pyramis* Hartman, 1886, Proc. Acad. Nat. Sci. Philadelphia, 1886: 34, pl. 2, fig. 12—Vate; Sykes, 1903, Proc. Malac. Soc. London, 5: 198—Terebu and Renee Rivers, Espiritu Santo(?); Pilsbry, 1909, Man. Conch., (2), 20: 281–282, pl. 33, fig. 7.

*Range*.—Vate (the Espiritu Santo record is not accepted).

*Material*.—Vate (CM 62.4305, holotype and paratype).

*Remarks*.—The aperture and body whorl of *P. pyramis* are more swollen and the whorls more rounded than in *P. eximia*. Otherwise the two species are very similar. The Espiritu Santo records for *P. pyramis* are probably based on specimens of *P. albescens* Hartman, if, indeed, the two should prove to be distinct.

### **Partula proxima** Hartman

*Partula proxima* Hartman, 1886, Proc. Acad. Nat. Sci. Philadelphia, 1886: 34, pl. 2, fig. 11—Vanua Lava, Banks Group; Pilsbry, 1909, Man. Conch., (2), 20: 286–287, pl. 34, figs. 12, 13.

*Range*.—Vanua Lava, Banks Group.

*Material*.—Type photograph (CM).

*Remarks*.—The type specimens are in the Australian Museum, Sydney. A photograph of the holotype in the Carnegie Museum was too faded to be reproduced. *P. proxima* is quite similar to *P. caledonica* but has sufficiently impressed sutures and elongate spire to be placed in the *pyramis* series. As mentioned in the discussion of *P. caledonica*, the record of that species from Vanua Lava may have been based on the specimens Hartman later described as *proxima*.

### **Partula eburnea** Hartman

*Partula eburnea* Hartman, 1886, Proc. Acad. Nat. Sci. Philadelphia, 1886: 33, pl. 2, fig. 10—no locality; Pilsbry, 1909, Man. Conch., (2), 20: 281, pl. 33, fig. 8.

*Range*.—Locality unknown.

*Material*.—No material available.

*Remarks*.—The type specimens are in the Australian Museum, Sydney. A note on a photograph (ANSP) indicates that Hartman

considered *P. eburnea* to be identical with *P. macgillivrayi*. *P. eburnea* has been placed in the *pyramis* series on the basis of its slender, produced spire and rounded whorls.

***Partula eximia* Hartman.** Plate 14, figs. 5, 6.

*Partula eximia* Hartman, 1886, Proc. Acad. Nat. Sci. Philadelphia, 1886: 35, pl. 2, fig. 14—Aneiteum (ex Thomson, Layard); Pilsbry, 1909, Man. Conch., (2), 20: 280–281, pl. 33, fig. 11.

*Range*.—Aneiteum.

*Material*.—Aneiteum (CM 62.4292, holotype and paratype).

*Remarks*.—*P. eximia* differs from *P. proxima* in being less obese and in having the body whorl more swollen.

***Partula albescens* Hartman.** Plate 14, figs. 7, 8.

*Partula albescens* Hartman, 1888, Proc. Acad. Nat. Sci. Philadelphia, 1888: pl. 13, fig. 4—Aure (=Aore) and Sitova (=Tutuba) Islands (Layard); Pilsbry, 1909, Man. Conch., (2), 20: 282–283, pl. 33, figs. 9–10.

*Range*.—Aore and Tutuba Islands off Espiritu Santo.

*Material*.—Aore (CM. 62.4290, holotype and paratypes); Tutuba (ANSP 60534); Aolia (=Aore?, Aoba?) (ANSP 144263); New Hebrides (USNM 608987 ex Quadras).

*Remarks*.—*P. albescens* comes close to forming a connecting link between the *macgillivrayi* and *pyramis* series. The shells from Tutuba (pl. 14, fig. 7) are shorter and proportionately broader, and have a narrower lip than those from Aore. Population studies may show that Tutuba has a local race, but taxonomic recognition on the basis of two shells is not warranted.

SUPERSPECIES OF *Partula auraniana*

Shell thin, smaller than the *macgillivrayi* and *pyramis* superspecies. A broad white band is below the suture; apex and spire brownish, fading to greenish-yellow on body whorl. Spiral sculpture prominent.

The coloration and strong spiral sculpture serve to separate the *auraniana* superspecies from the other two. The *auraniana* complex has not yet been found in the central and southern New Hebrides.

***Partula auraniana* Hartman.** Plate 15, figs. 1, 2, 6.

*Partula auraniana* Hartman, 1888, Proc. Acad. Nat. Sci. Philadelphia, 1888: 250, pl. 13, fig. 1—Aore Island; Sykes, 1903, Proc. Malac. Soc. London, 5: 198—Lo and Hiu Islands, Torres Group (J. J. Walker); Ancy, 1905, Nautilus, 19, (4), p. 44—Buka-Buka, Torres Group; Pilsbry, 1909, Man. Conch., (2), 20: 284–285, pl. 34, figs. 7–10.

*Range*.—Aore near Espiritu Santo and Lo, Hiu, and Buka-Buka Islands in the Torres Group.

*Material*.—Aore (CM 62.4295, holotype and paratype; UMMZ 145681, ex B. Walker, Tomlin); Hiu Island (UMMZ 145682, ex B. Walker, Tomlin, Sykes).

*Remarks*.—*P. auraniana* is smaller and has fewer whorls than *P. fraterna* Hartman and *P. carnicolor* Hartman. The holotypes of the three species seem quite different, but enough intergradation could be found among the paratypes to make it probable that the "species" represent infraspecific variations rather than distinct species. Sykes (1903, p. 198) considered that the specimens from Lo Island, Torres Group, represented a local race. I saw no material from this island.

***Partula fraterna* Hartman.** Plate 15, figs. 3, 4.

*Partula fraterna* Hartman, 1888, Proc. Acad. Nat. Sci. Philadelphia, 1888: 250, pl. 13, fig. 2—Aore Island; Sykes, 1903, Proc. Malac. Soc. London, 5: 198—Ravenga, Vanua Lava and Lakona, Gaua (Banks Group); Pilsbry, 1909, Man. Conch., (2), 20: 285-286, pl. 34, fig. 4.

*Range*.—Aore, Vanua Lava, and Gaua.

*Material*.—Aore (CM 62.4294, holotype and paratype).

*Remarks*.—*P. fraterna* has more whorls, and a more capacious umbilical fissure, and is larger than *P. auraniana*. *P. carnicolor* is larger and more obese, and has a columellar situation which is lacking in *P. fraterna*. No specimens of *P. fraterna* from the Banks Islands were seen.

***Partula carnicolor* Hartman.** Plate 15, figs. 5, 9.

*Partula carnicolor* Hartman, 1888, Proc. Acad. Nat. Sci. Philadelphia, 1888: 250, pl. 13, fig. 3—Aore Island; Pilsbry, 1909, Man. Conch., (2), 20: 286, pl. 34, figs. 1-3.

*Range*.—Aore Island.

*Material*.—Aore (CM 62.4289, holotype and paratype).

*Remarks*.—The size, elongate spire, and columellar situation separate *P. carnicolor* from *P. auraniana* and *P. fraterna*. The paratype (see Table II) is much smaller than the holotype and forms a connecting link with other members of the *auraniana* superspecies.

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The second series of *Partula* is found in northern Melanesia. Two species (*P. minor* Hartman and *P. milleri*, new sp.) have been re-

ported from the New Hebrides. *P. minor* may be a mislabeled Solomon Island specimen, but *P. milleri* represents a valid record from Espiritu Santo. *P. vanikorensis* from the Santa Cruz Islands also belongs here.

**Partula minor** Hartman. Plate 15, fig. 7.

*Partula minor* Hartman, 1886, Proc. Acad. Nat. Sci. Philadelphia, 1886: 31, pl. 2, fig. 5—Erromanga (doubtful); Pilsbry, 1909, Man. Conch., (2), 20: 287-288, pl. 34, figs. 5, 6, 14.

*Range*.—Erromanga(?).

*Material*.—Erromanga (CM 62.4243, holotype and paratype).

*Remarks*.—*P. minor* is very similar to *P. pellucida* Pease and *P. coxi* Pease from the Solomon Islands. The sculpture of the last two "species" is more prominent than that of *P. minor*, but otherwise they are similar. Hartman (1886) described *P. hastula* and *P. minor* from Erromanga. Later, the type lot of *P. hastula* was found to have been collected on Eddystone Island in the Solomons. It is possible that *P. minor* has an erroneous locality, but until Erromanga has been explored for partulids, it would be better to consider *P. minor* a dubious member of the New Hebridean fauna, instead of rejecting the locality completely.

**Partula milleri**, new species. Plate 15, fig. 8; plate 16, fig. 4.

A species of *Partula* separated from *P. regularis* Hartman and *P. minor* Hartman by its very strong spiral sculpture, prominent suprasutural cord, and obese shape.

Shell ovate-conic, thin, translucent, nearly devoid of color. Whorls  $4\frac{3}{4}$ , rounded, without trace of a carina. Sutures lightly impressed. Body whorl laterally compressed behind the aperture. Sculpture of numerous dense, wavy, spiral lines distinctly narrower than the interstices. A very prominent suprasutural cord on all but embryonic whorls. Aperture ovate, parietal callus thick, slightly opaque. Columellar wall less angulate than in *regularis*. Lip expanded, thickened internally. Umbilicus open. Height 15.8 mm., diameter 9.1 mm., aperture 8.6 by 5.4 mm.

*Type*.—United States National Museum no. 619738. Collected on the south side of Pallikula Bay, Espiritu Santo, New Hebrides, by Walter B. Miller.

*Remarks*.—*P. milleri* is most closely related to *P. regularis* Hartman from Guadalcanal in the Solomons. *P. regularis* is less obese, has a less prominent suprasutural cord and weaker spiral sculpture in which the striae are as wide as their interstices. *P. milleri* is the first species of the northern Melanesian type of *Partula* to be definitely reported from the New Hebrides.



It is named after the collector, Commander Walter B. Miller of Falls Church, Virginia.

**Partula vanikorensis** (Quoy and Gaimard). Plate 12, figs. 1, 2.

*Helix vanikorensis* Quoy and Gaimard, 1832, Voy. l'Astrolabe, Zool., 2: 116, pl. 9, figs. 12-17—Vanikoro, Santa Cruz Islands (found under the leaves of trees at the abandoned village of Ocili).

*Partula vanikorensis* (Quoy and Gaimard), Pilsbry, 1909, Man. Conch., (2), 20: 289-290, pl. 35, figs. 15-17.

*Range*.—Vanikoro, Santa Cruz Islands.

*Material*.—Vanikoro (MCZ 24844, MCZ 192352, ex Stevenson, Fox).

*Remarks*.—On the basis of the figures in Quoy and Gaimard (1832-35), I had considered that *vanikorensis* might belong to the genus *Samoana* Pilsbry (1909). Of the two available specimens, one (MCZ 24844 ex British Museum) is probably a mislabeled *Partula otaheitana sinistrorsa* Pease from Tahiti, and the other (MCZ 192357) was very similar to *Samoana alabastrina* (Pfeiffer) from Fiji (CM 62.4293, cotypes of *Partula nematoraphe*). The Vanikoro specimen had a less widely reflexed columellar whorl, much less prominent suprasutural cord, stronger spiral sculpture, and a more thickened lip. The apical sculpture is like that shown for *Partula attenuata* Pease (see Pilsbry, 1909, pl. 24, fig. 3).

Photographs of the type and a cotype furnished by Dr. André Franc of the Paris Museum (pl. 12, figs. 1, 2) showed specimens completely different from the figures in Quoy and Gaimard, and very similar to *Partula milleri* in general appearance. The specimens are so unlike the original figures that it is difficult to believe that there has not been an error, either in the illustrations or in the selection of type specimens.

Without new material from Vanikoro and personal examination of all the Paris Museum Partulidae, it is impossible to clarify the identity of *Helix vanikorensis* or the status of the Vanikoro population. As a temporary expedient, they are grouped under the name *Partula vanikorensis* (Quoy and Gaimard).

Iredale (1927, p. 74) reported that a *Partula* was collected on Santa Cruz Island, but it has never been described or figured.

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Several species of partulids have been erroneously reported as coming from the New Hebrides. Others were so inadequately de-

scribed and figured that they cannot be recognized. References are included for completeness.

### **Partula concinna** Pease

*Partula concinna* Pease, 1871, Amer. Jour. Conch., 7: 196—Tanna (Cox); Hartman, 1886, Proc. Acad. Nat. Sci. Philadelphia, 1886: 35, pl. 2, fig. 16; Pilsbry, 1909, Man. Conch., (2), 20: 288, pl. 36, figs. 9, 12.

Hartman's single specimen (CM 62.4244, ex Hartman, Taylor) from "Tanna" probably is a mislabeled *Partula taeniata nucleola* from Moorea, Society Islands (see Pilsbry, 1909, p. 288, and H. H. Smith, 1902, p. 455).

### **Partula glaber** Hartman

*Partula glaber* Hartman, 1885, Proc. Acad. Nat. Sci. Philadelphia, 1885: 205, 1 fig.—no locality except "New Hebrides(?)."

This is the Peruvian *Drymaeus strigatus*, var. *purus* (Pilsbry, 1909, p. 319).

### **Partula hastula** Hartman

*Partula hastula* Hartman, 1886, Proc. Acad. Nat. Sci. Philadelphia, 1886: 33, pl. 2, fig. 9—Erromanga, Solomon Islands (sic) (Brazier); Pilsbry, 1909, Man. Conch., (2), 20: 291, pl. 35, figs. 6–8—Simbo, Eddystone Island, Solomon Islands.

The correction of type locality is based on a note in Hartman's handwriting found with the original label.

### **Partula hollandiana** Pilsbry

*Partula hollandiana* Pilsbry, 1909, Man. Conch., (2), 20: 293–294, pl. 37, figs. 8–10—locality unknown.

This is very similar to *Partula regularis* Hartman from Guadalcanal, Solomon Islands, and may be a local race of that species.

### **Partula nematoraphe** Pilsbry

*Partula nematoraphe* Pilsbry, 1909, Man. Conch., (2), 20: 279–280, pl. 35, figs. 1–3—unknown locality, "but the shell has wholly the appearance of the New Hebridean *Partulae*."

Pilsbry and Cooke (1934a, p. 17) synonymize this species with *P. alabastrina* Pfeiffer from Moala, Fiji Islands.

### **Partula repanda** Pfeiffer. Plate 9, fig. 7.

*Partula repanda* Pfeiffer, 1855, Proc. Zool. Soc. London, 1855: 98—New Hebrides (Cuming collection); Pilsbry, 1909, Man. Conch., (2), 20: 288–289, pl. 34, fig. 11.

Hartman considered that *Partula repanda* might be related to the pale varieties of *P. recta* Pease from the Marquesas, but comparison of *recta* with the type of *repanda* in the British Museum indicated that they were distinct (see H. H. Smith, 1902, p. 459). The photograph of the holotype (pl. 9, fig. 7) shows a shell that resembles the Society Island partulid more than any Melanesian species.

### **Partula turricula** Pease

*Partula turricula* Pease, 1871, Amer. Jour. Conch., 7: 196—New Hebrides(?) (received from Cox); Pilsbry, 1909, Man. Conch., (2), 20: 283–284.

The lack of transverse striae and the sinistral coiling separate *P. turricula* from *macgillivrayi* and *caledonica*. The location of the type of *P. turricula* is unknown and the species has never been figured.

## Order SIGMURETHRA Pilsbry, 1900

Snails in which the ureter of the kidney is abruptly reflexed, passing to the posterior end of the lung cavity. An open groove or closed tube (secondary ureter) continues across to the last fold of the gut, then follows it forward to the mantle edge. (After Pilsbry, 1900a, pp. 562–563.)

Family relationships within the Sigmurethra are complex and little understood. The dominant land snails of continental areas belong to the Sigmurethra and adaptive radiations have been numerous and extensive. Much of the confusion as to distribution and relationships has resulted from the refusal of certain conchologists to recognize that species whose shells differ because of ecological adaptations may actually be very closely related (see Pilsbry, 1894, pp. viii, xiv). Conversely, strikingly similar shells may belong to different families and resemble each other only because they are adapted for similar ecologic niches. The shells of land snails are very plastic, and form alone is unreliable in classification.

Use of the divisions Aulacopoda and Holopoda (see p. 36) recognizes two major overlapping distributional patterns which probably reflect a basic evolutionary divergence.

## Suborder AULACOPODA Pilsbry, 1896

Sigmurethrous snails in which the pedal groove is conspicuously impressed and situated well above the lateral angle of the foot, which is bordered by a band of the sole (Pilsbry, 1946b, p. 231).

Pilsbry (1896, p. 110) recognized two family groups in the Aulacopoda. Division I, containing the Zonitidae, Helicarionidae, and

Limacidae, was named the superfamily Limacacea by H. B. Baker (1941, p. 206); division II, containing the Endodontidae, Arionidae, and Philomycidae, was called the superfamily Arionoidea by H. B. Baker (1955, p. 109). The name Arionoidea is here emended to Arionacea to conform with the usual superfamilial endings.

Shell-bearing limacoids and arionoids differ in the general appearance of the shell, but anatomical differences between the superfamilies are small because of convergent evolution in slug taxa. The most constant difference is in the shape of the marginal teeth. The Limacacea have marginal teeth with narrow, elongate, basal plates and the teeth are unicuspid or bicuspid as a result of the elevation of the outer cusp on the middle cusp. The Arionacea have marginal teeth with short, squarish, basal plates and with either one or several cusps.

Radular teeth are usually of little value in delineating categories at the family level, but the Limacacea and Arionacea have slug taxa which are convergent in most other characters. The persistent primitiveness of the marginal teeth in the Aulacopoda, despite the great divergence in centrals and laterals, is in keeping with the law of meso-metamorphosis: "All modifications in the teeth proceed from the median line of the radula outwards toward the edges, the outer marginal teeth being the last to be modified." (Pilsbry, 1894, p. xiii.) The Limacacea and Arionacea have shells which are easily distinguished, while the slugs can be separated by anatomical details. Despite the convergent slug taxa, recognition of the two superfamilies seems both desirable and valid.

Both the Limacacea and Arionacea are represented in the New Hebrides. With very few exceptions, the Limacacea are at their southern limit of distribution, but the Arionacea are important constituents of the fauna of New Caledonia and New Zealand. On the basis of distribution and unspecialized structure, it seems probable that the Arionacea are the more primitive taxon and stand nearer the sigmurethran ancestor than either the Limacacea or the Holopoda (Pilsbry, 1894, p. xxxix). On continental areas the shell-bearing limacoids are much more numerous, and they appear to be replacing the shell-bearing arionids. The latter still seem to be dominant in Tasmania, New Zealand, New Caledonia, and many oceanic islands.

### Superfamily ARIONACEA

Marginal teeth with short, wide and squarish basal-plates with one or several cusps, the outer cusp never elevated on middle cusp (Pilsbry, 1896, p. 110).

Two of the three families, the Arionidae and Philomycidae, are of limited distribution and obviously derived from the third family, the Endodontidae.

The Arionidae are Holarctic, with genera in Europe, Asia (*Arion* in Siberia and *Anadenus* in the Himalayas and China), western North America, northern Africa, and South Africa (*Oopelta*) (Pilsbry, 1948, p. 661). They are restricted to areas of high humidity and seem far less adaptable than either the limacoid or the helicoid slugs. A few species of *Arion* have been disseminated by commerce. In the more humid, temperate regions of America, South Africa, New Zealand, and Australia they have become well established.

In the Philomycidae the mantle covers the entire body, and the shell has been completely lost. *Philomycus* is restricted to eastern North America from Canada to Florida and northeastern Texas. *Pallifera* is found in the northeastern United States as far south as North Carolina and in Central America from Mexico to Colombia (Pilsbry, 1948, pp. 748-770). *Meghimatium*, which is very closely related to *Pallifera*, is found in Japan, China, Tonkin, India, and Indonesia east to Borneo and the Celebes (van Benthem Jutting, 1952, p. 424). The ecological relationship between *Meghimatium* and the veronicellid slugs is unknown. It is not improbable that they compete, since both are vegetarians and restricted to similar humid situations.

The Endodontidae probably are the most primitive living sigmurethrans. They certainly represent the most widely distributed family of land mollusks. Unfortunately, the minute size of the animals and their distribution in the Southern Hemisphere has prevented any extensive survey of the entire family as to anatomical structure. Recent studies (Iredale, 1913, 1915, 1933, 1937a; Suter, 1913; and Dell, 1952a) have shown that many taxa are well characterized by sculptural differences of the shells. I found it necessary to make a comprehensive survey of the Pacific Endodontidae in order to place the New Hebridean species in genera.

### Family ENDODONTIDAE

Shell umbilicate, depressed-heliciform to discoidal, many species flammulate or banded. Aperture rounded-lunate or compressed, lamellate in many species; peristome sharp, expanded only near the columellar margin. Sculpture of various combinations of radial, spiral, or oblique ribs and/or striae. Foot with pedal grooves meeting above the tail; sole not divided longitudinally. Lung without noticeable venation other than the pulmonary vein. Kidney triangular, squarish, or U-shaped. Genitalia simple; spermatheca on a long duct. Jaw arcuate, entire,

or formed of loosely connected squarish plates. Rachidian tooth tricuspid, narrower than or nearly equal to the laterals. Laterals bi- or tri-cuspid; marginals with wide, short basal plates and one to several cusps. (Modified from Pilsbry, 1948, pp. 565-566.)

Intergeneric relationships of the Endodontidae are very poorly understood. Iredale (1937a) recognized by implication at least six families, while Thiele (1931) divided the single family into eight subfamilies. As emphasized by Pilsbry (1948, p. 566), the anatomy of only a very few genera is known. Although two markedly distinct subfamilies can be recognized, most of the genera must still be placed in a large subfamily, the Endodontinae.

Species with the jaw formed by loosely connected plates belong to the subfamily Punctinae Morse, 1864 (=Laominae Suter, 1913), which Iredale (1937a) raised to family rank. The Punctinae (fig. 13) include the Holarctic and South African *Punctum*, Neotropical *Radiodiscus*, Australian "Laomidae" (Iredale, 1937a, 1939), New Zealand "Laomidae" (Powell, 1946a), Kermadec Island *Paralaoma* (Iredale, 1913), and probably the New Hebridean *Phrixgnathus* reported below.

The North American *Helicodiscus* and Mexican *Chanomphalus* include discoidal species in which the whorls do not substantially increase in size. Possibly *Polygyriscus* Pilsbry (1948, p. 1097) also belongs to the Helicodiscinae. *Stenopylis* (fig. 24) from the Indo-Melanesian region (see Solem, 1957) has very similar shell structure, but also a prominent rachidian tooth, less prominent endo- and ectocones on the laterals, and a jaw composed of separate(?) plates. The difference between the jaws of *Stenopylis* and *Helicodiscus* is partially bridged by the stegognath jaw of *Hebetodiscus*, a subgenus of *Helicodiscus* (see Pilsbry, 1948, p. 635). Further study may indicate that *Stenopylis* should be placed in the Helicodiscinae, rather than in a separate subfamily (Thiele, 1931, p. 569) or family (Iredale, 1937b, pp. 1-2).

For the other genera, there seem to be no criteria by which easily recognizable subfamilies can be delineated. Suter (1913) attempted to divide the New Zealand species into families based on the presence (Flammulinidae) or absence (Endodontidae) of a caudal foss. H. B. Baker (1941, p. 205) and Pilsbry (1896, p. 109, and 1946b, p. 232) have pointed out the slight utility of the caudal foss in taxonomy, and Suter's divisions are not accepted here.

In regard to the generic affinities of the Pacific "Endodontinae," numerous changes seem necessary. Essentially there are four types of apical sculpture found in the Pacific species: radial ribs only; radial

and spiral ribs; spiral ribs; and smooth apical whorls. It is probable that the species with smooth apices were derived from one of the other three types, and other characters will have to be used to determine their exact affinities. When used in conjunction with the subsidiary characters of apertural armature and shape, a reasonably logical classification results. Full elucidation of the classification is not possible at this time, but the broad outlines are an important preamble to the zoogeographic survey.

The sculpture of spiral striae is found throughout most of the Pacific. In the Indonesian region there is the minute toothed *Beilania* (see Solem, 1957) which is probably ancestral to all the Micronesian species. *Beilania* (fig. 25) possibly reaches New Guinea and the Bismarcks but not Australia or Polynesia. In Polynesia, New Zealand, western Australia, the Solomon Islands, and the New Hebrides there is a larger toothless series of species which have relatively few spiral ribs on the apical whorls. The earliest name for this group seems to be *Mocella* Iredale, 1915 (fig. 25). In New Caledonia and eastern Australia (including Tasmania) species with many more spiral ribs are found (fig. 25). On the basis of evidence from the Micronesian derivatives of *Beilania*, it seems probable that the pattern of few spiral lines is primitive, that of many spiral lines advanced (see p. 298). Consideration of the interrelationships of the New Caledonian and East Australian species is well beyond the scope of this study.

The radially ribbed apical sculpture is represented by two main groups, *Discocharopa* and *Ptychodon*. *Discocharopa* (fig. 24) is minute, greasy white in color, usually very widely umbilicate, and either toothed or toothless (see Solem, 1957). *Ptychodon* is larger, horn-colored or flammulated, has many apertural lamellae and a narrower umbilicus. It is found in Polynesia and New Zealand (fig. 26). A few Australian species with radially ribbed apices have been placed in "genera" by Iredale and are not considered at this time.

The species with both radial and spiral ribs on the apical whorls form two series. In the Indonesian–New Guinean complex (Solem, 1958b) the ribs are much modified; in the New Hebridean endemic, *Reticharopa*, the radial and spiral ribs are nearly equal in size. Possibly the New Guinean endemic, *Paryphantopsis*, is derived from the Indonesian forms with radial and spiral ribs (see Solem, 1958b).

Of the taxa with smooth apical whorls the New Zealand *Charopa* (fig. 24) may be derived from *Mocella*, and *Endodonta*, *Nesophila*, and *Nesodiscus* from *Ptychodon* (see figs. 24, 26).

The above sketch of generic affinities gives no idea of relationships between the taxa with different types of apical sculpture and only a brief outline of the distribution and classification. It is hoped that study of this family can be pursued at a later date with more material than is available at the present time.

The New Hebridean Endodontidae belong to four genera: the endemic *Reticharopa*; the punctid genus *Phrixgnathus*, found elsewhere only in New Zealand; *Mocella*, which ranges throughout most of Polynesia, Melanesia, New Zealand, and western Australia; and *Discocharopa*, which has a scattered distribution from the Philippines to the Kermadec Islands.

Of the nine species which I've examined, only three had been previously described. Five of the nine were found only in stream drift deposit (ML 95) on Espiritu Santo. A key, based on apical sculpture and number of ribs, is given below. There are published records for one additional species, *Charopa perryi* Smith, which has never been figured.

#### Key to the New Hebridean Endodontidae

1. Body whorl keeled; no prominent radial ribs; apex smooth.....2  
    Body whorl rounded or angulated; with prominent radial ribs; apex with distinct sculpture (except in worn specimens).....3
2. Body whorl sharply carinated; diameter 6 mm.  
    *Phrixgnathus tenuiscripta* (Ancey)  
    Body whorl bluntly keeled; diameter less than 5 mm.  
    *Phrixgnathus glissoni* (Ancey)
3. Spire elevated or in plane of body whorl.....4  
    Spire distinctly depressed.....*Reticharopa* sp.
4. Apical sculpture of radial ribs or reticulated.....5  
    Apical sculpture of spiral ribs only.....*Mocella euryomphala*, new sp.
5. Apex reticulated; umbilicus contained more than three times in diameter...6  
    Apex radially ribbed; umbilicus contained twice in diameter.  
    *Discocharopa planulata*, new sp.
6. Ribs on body whorl 35-40.....7  
    Ribs on body whorl more than 65.....8
7. Body whorl angulated; diameter 3 mm.; Aneiteum...*Reticharopa geddiei*, new sp.  
    Body whorl rounded; diameter 2 mm.; Espiritu Santo.  
    *Reticharopa latecosta*, new sp.
8. Ribs on body whorl 70-75; Espiritu Santo...*Reticharopa stenopleura*, new sp.  
    Ribs on body whorl about 110; Aneiteum.....*Reticharopa helva* (Cox)

#### Subfamily PUNCTINAE

#### Genus PHRIXGNATHUS Hutton, 1883

Shell imperforate to widely umbilicate, trochoidal to planulate, body whorl rounded to sharply keeled. Sculpture smooth to strongly radially ribbed. Aper-



ture toothless. Animal without caudal mucous pore. Jaw composed of papillose, imbricating plates. Radula with narrow uni- or tri-cusped central tooth, bicuspid laterals, and low, wide, bicuspid marginals. (Adapted from Suter, 1913, p. 733.)

*Type species.*—*Phrixgnathus celia* Hutton.

*Remarks.*—Detailed study of the New Zealand *Phrixgnathus* may indicate that the genus, as now constituted, is polyphyletic. However, inspection of the material in the University of Michigan Museum of Zoology suggests that a complete series of transitional species exists between the smooth, trochoidal type, *P. celia*; the radially ribbed, helicoid *P. allochroida* Suter; and the smooth, planulate, widely umbilicate *P. sciadium* (Pfeiffer). The soft parts of very few species have been examined and divisions based on anatomical features are not yet possible.

Two New Hebridean "*Endodonta*," *glissoni* Ancey and *tenuiscripta* Ancey, are very similar to *Phrixgnathus sciadium*. Although the animals have not been studied, the conchological similarity is so great that I feel little hesitation in placing them in *Phrixgnathus*. *Phrixgnathus glissoni* is easily separated from *P. tenuiscriptus* by the larger size and sharp, not rounded, carina of the latter species.

***Phrixgnathus glissoni* (Ancey).** Plate 28, figs. 3-5.

*Patula glissoni* Ancey, 1889, *Le Naturaliste*, 11: 50—Sea View Estate, Vate Island (Glisson!).

*Endodonta glissoni* Ancey, 1896, *Nautilus*, 10, (8), p. 90.

*Range.*—Vate, Espiritu Santo.

*Material.*—ML 68, ML 95; Vate (UMMZ 136690, ex Walker, Ponsonby, Layard, from the type lot).

*Remarks.*—The few specimens examined show a considerable range of variation in whorl convexity, degree of carination, and H/D ratio. Ancey's variety "B" represents one of the more trochoidal, less sharply carinate specimens, and is probably taxonomically insignificant. No constant differences could be found between the Espiritu Santo and Vate shells. The larger specimens have  $4\frac{1}{4}$  to  $4\frac{1}{2}$  whorls and are 4.5 to 4.8 mm. in diameter.

***Phrixgnathus tenuiscriptus* (Ancey).** Plate 28, figs. 1, 2.

*Endodonta tenuiscripta* Ancey, 1896, *Nautilus*, 10, (8), p. 90—Malekula (ex Layard); Ancey, 1905, op. cit., 19, (4), p. 42.

*Range.*—Malekula, Espiritu Santo.

*Material.*—ML 95.

*Remarks.*—A single, broken, juvenile specimen ( $3\frac{1}{2}$  whorls) seems referable to *tenuiscriptus*. The knife-edge keel and close-set radial ribs of the shell easily separate *tenuiscriptus* from *glissoni* and were the characters used by Ancey in his original diagnosis. In *P. glissoni* the keel is rounded; there is a supracarinal groove; the sculpture consists of a few indistinct, broad ribs at irregular intervals; and the shell is about 4.7 mm. in diameter. In *P. tenuiscriptus* the keel is produced into a knife-edge carina; the sculpture consists of prominent, close-set radial ribs at regular intervals; and the shell is about 6.5 mm. in diameter with five whorls (Ancey, 1896, p. 90).

### Subfamily ENDODONTINAE

#### Genus DISCOCHAROPA Iredale, 1913

Shell minute, widely umbilicated, discoidal, with numerous very close-set radial ribs. Apical sculpture continued on rest of shell. No spiral sculpture. Aperture toothed or toothless.

*Type species.*—*Discocharopa exquisita* Iredale.

*Remarks.*—Several species from various parts of the Pacific are grouped under *Discocharopa*. They agree in sculpture, discoidal shape, and usually wide umbilicus. The aperture is toothed in two species, *D. exquisita* Iredale and *D. werneri* Solem (1957), and toothless in the others. The anatomy is unknown. Several specimens of a *Discocharopa* were found in stream drift collected on Espiritu Santo. Comparisons with paratypes of most of the other species indicated that they belong to a new species which is described below.

#### *Discocharopa planulata*, new species. Plate 32, figs. 1–3.

A species of *Discocharopa* characterized by its slightly elevated spire, very close-set radial ribs, relatively gradual whorl increase, and toothless aperture.

Shell minute, discoidal, spire only slightly raised above plane of body whorl. Whorls 3–4, gradually increasing in size. Aperture ovate, slightly flattened above. Umbilicus widely open, shallow, contained 1.96 times in the diameter. Sculpture of numerous close-set, slightly retractive radial ribs; about 145 on body whorl. Interstices with several very fine radial riblets. No spiral sculpture. Diameter of holotype 1.45 mm., lesser diameter 1.29 mm., height 0.55 mm., with  $3\frac{3}{4}$  whorls.

*Type.*—University of Michigan Museum of Zoology no. 186037. Collected from stream drift in the Sarakata River Valley, Espiritu Santo (ML 95), by Robert E. Kuntz in May, 1944.

*Paratypes.*—From ML 95, specimens distributed as follows: UMMZ 186036, CNHM 54904, BPBM 212378, MCZ 186826.

*Remarks.*—*Discocharopa planulata* differs from the Kermadec Island *D. exquisita* by its toothless aperture, more closely set ribs, and slightly elevated spire; it differs from the Indonesian *D. microdiscus* van Benthem Jutting by its less rapidly increasing whorls and less elevated spire.

### Genus **MOCELLA** Iredale, 1915

Small, tightly coiled shells with slightly elevated spire. Umbilicus moderately open, deep. Apical sculpture of 8 to 12 spiral striae; spire and body whorl with slightly retractive radial ribs. Interstices with fine radial riblets crossed by spiral striae (pl. 31, fig. 4). Aperture toothless, ovate; apertural edge slightly flattened above.

*Type species.*—*Helix corniculum* Reeve (= *Mocella cogitata* Iredale, 1941, p. 91).

*Remarks.*—*Mocella* is equivalent to *Charopa* as used in previous publications on the endodontids of Melanesia and Polynesia. *Charopa* must be restricted to New Zealand species that have smooth apical whorls. The Polynesian and Melanesian species have spirally striated apices, as do the New Zealand species that Iredale placed in *Mocella*. In the absence of conflicting evidence, they are considered congeneric. It is probable that the west Australian species that Iredale (1937a) placed in *Luinodiscus* are not more than subgenerically separable.

Species belonging to *Mocella* have been found from the Bismarcks to the Society Islands, but are not known from the Tuamotus, Marquesas, Australs, or New Caledonia. Several shells from Espiritu Santo represent the following new species:

***Mocella euryomphala***, new species. Plate 6, figs. 7, 8; plate 31, figs. 1–5.

A species of *Mocella* most similar to *M. solomonensis* (Clapp) but easily separated from that and all other species by the comparatively large umbilicus.

Shell small, depressed-helicoid, spire only slightly elevated. Whorls  $3\frac{3}{4}$  to  $4\frac{1}{8}$ , tightly coiled, gradually increasing in size, sutures deeply channeled. Aperture ovate, flattened dorso-laterally. Umbilicus open, deep, contained about 3.2 to 3.5 times in the diameter. Apical whorls  $1\frac{1}{2}$ , with about eleven spiral ribs (pl. 31, fig. 5). Spire and body whorl with strong radial ribs (ca. 90 on body whorl). Numerous fine riblets crossed by spiral lines between primary ribs (pl. 31, fig. 4). Color light reddish-horn. Diameter 2.5 to 2.8 mm., height 1.3 to 1.4 mm.

*Type.*—University of Michigan Museum of Zoology no. 186042. Collected at Brigstock Point, Espiritu Santo, New Hebrides (ML 63), under logs, by Robert E. Kuntz on April 25, 1944.

*Paratypes*.—On Espiritu Santo, Kuntz collected specimens at the following stations: ML 40, ML 63 (type locality), ML 78, and ML 95. Paratypic specimens are CNHM 54906, MCZ 186828, BPBM 212379, and ANSP. An additional shell from Espiritu Santo (USNM 432458, Harrington!) is also a paratype.

*Remarks*.—Many “species” of *Mocella* will probably be synonymized when the genus has been critically reviewed. *M. euryomphala* was compared with all the New Zealand and most of the Polynesian species. On the basis of sculpture it is closest to *M. solomonensis*, but in shape and general appearance it more nearly resembles some of the Polynesian species. The relatively wide umbilicus is diagnostic and at once separates *M. euryomphala* from the other species of *Mocella*.

Lot ML 63 was collected alive under bark on a rotting log in deep shade. Fully satisfactory dissections of the animal were not obtained, but I extracted and studied the terminal portions of the male genitalia, jaw and radula. No other “*Charopa*” except the aberrant New Zealand species *Egestula egesta* (Gray) has been dissected (see Suter, 1913). It has an epiphallallic flagellum, different insertion of the penial retractor, and less swollen penis.

In *Mocella euryomphala* the foot is not divided longitudinally but has pedal grooves with a distinct pit where they meet over the tail. Iredale (1913, pp. 375–376) probably mistook the caudal pit for a true “mucous gland” in some Kermadec Islands endodontids. The jaw of *M. euryomphala* is membranous and solid, but without radial striae. There are slight indications of concentric growth rings and a low median projection. The radula (pl. 6, fig. 7) has the formula 12–6–1–6–12 in the single specimen examined. The central and lateral teeth are poorly differentiated, both with three cusps; the mesocone, by far the largest, is as long as the basal plate. The marginals are subequally tricuspid, thus agreeing well with the teeth of *Mocella corniculum* (Reeve) (see Suter, 1913, p. 726).

The male genitalia of *M. euryomphala* (pl. 6, fig. 8) are remarkable mainly for their swollen, sharply differentiated epiphallus. In the other species of endodontids from the Pacific (both in *Egestula* and *Endodonta*), the epiphallus is not sharply demarcated from the penis and the penial retractor inserts at the junction of the vas deferens and epiphallus rather than at the penial-epiphallallic angle. Comparison should be made with the anatomy of *Endodonta* (Cooke, 1928) and the North American *Anguispira* (Pilsbry, 1948, p. 568).

Details of the female and internal structure of the male genitalia were not worked out.

### RETICHAROPA, new genus

Small, toothless, deeply umbilicated shells with slightly elevated spire. Whorls 3-4, sutures moderately impressed, last whorl descending slightly in front. Apical sculpture reticulate (pl. 31, figs. 6, 7), formed by radial and spiral ribs. Same sculpture continued on body whorl with decrease in size (or actual loss) of spiral ribs. Aperture ovate, with thin parietal callus, lip simple, not reflexed or thickened. Animal unknown.

*Type species.*—*Reticharopa latecosta*, new species.

*Remarks.*—*Reticharopa* is proposed for five species of New Hebridean "Charopa" that have reticulate apical sculpture (pl. 31, figs. 6, 7). In most species, the spiral ribs of the apex are continued over the radial ribs on the spire and body whorl, although they are greatly reduced on the post-apical whorls of *R. stenopleura*. *Reticharopa* is closely allied to an Indonesian-New Guinean genus (*Parvicharopa*), which differs from *Reticharopa* in having the spiral and radial ribs fused (see Solem, 1958a), more loosely coiled whorls, and a less elevated spire. It is possible that collections from the Bismarcks, the Solomons, and New Guinea will contain species which are intermediate between the Indonesian and New Hebridean groups.

Three of the five species of *Reticharopa* were recovered from a single drift sample (ML 95); the fourth species, *R. geddiei*, was found on Aneiteum in a specimen of *Placostylus fuliginus*; and the fifth species, *R. helva* (Cox), is also from Aneiteum.

### *Reticharopa geddiei*, new species. Plate 29, figs. 4-6.

A species of *Reticharopa* characterized by its large size (3 mm.), widely spaced radial ribs (35-40 on body whorl), prominent spiral ribs, and angulated body whorl.

Shell small, solid, deeply umbilicate, base convex. Whorls 4, rounded, increasing regularly in size; body whorl angulated, slightly descending in front. Sutures well marked, but only slightly impressed. Apical sculpture partially eroded. Spire and body whorl with widely spaced, retractive, radial ribs crossed by numerous (ca. 23 on third whorl) spiral ribs. Several riblets between the primary radial ribs. Aperture subquadrangulate, lip simple, not reflexed or thickened. Parietal callus thin. Umbilicus 0.75 mm. wide, open to the apex, contained about 4 times in the diameter. Diameter 3.1 mm., height 1.8 mm.

*Type.*—Chicago Natural History Museum no. 72335. Collected on Aneiteum Island.

*Remarks.*—The unique holotype was stuck in some dirt in the aperture of a specimen of *Placostylus fuliginosus*. *R. geddiei* most closely resembles *R. latecosta*, but it is easily separable by its larger size and angulated body whorl. The other endodontid known from Aneiteum, *Reticharopa helva* (Cox) (see p. 87), has a rounded body whorl and much more crowded ribbing.

*R. geddiei* is named after the pioneer missionary on Aneiteum, the Rev. John Geddie of Nova Scotia.

***Reticharopa latecosta*, new species. Plate 29, figs. 1–3.**

A species of *Reticharopa* characterized by its widely spaced primary ribs (35 on last whorl), prominent spiral ribs, rounded body whorl, and minute size (2 mm.).

Shell small, thin, deeply but narrowly umbilicate, spire slightly elevated. Whorls 4 to  $4\frac{1}{4}$  (holotype), gradually increasing in size, last whorl descending in front. Sutures deeply impressed. Apical whorls  $1\frac{1}{2}$ , sculpture composed of equally prominent radial and spiral ribs (pl. 31, fig. 6). Primary ribs slightly retractive and more widely spaced on body whorl and spire than on the apex. Spiral ribs continued over primary radials. Numerous secondary riblets between primary radials. Aperture ovate, lip simple, not thickened or reflexed. Parietal callus very thin. Umbilicus 0.5 mm. wide, contained four times in the diameter. Diameter of holotype 2.0 mm., height 1.1 mm.

*Type.*—University of Michigan Museum of Zoology no. 186040. Collected from stream drift in the Sarakata River Valley, Espiritu Santo, New Hebrides (ML 95), by Robert E. Kuntz, May–June, 1944.

*Paratypes.*—Paratopotypes are UMMZ 186041, BPBM 212376, and MCZ 186829.

*Remarks.*—*R. latecosta* has the same sculpture as *R. geddiei*, but the latter is easily recognized by its larger size, only slightly impressed sutures, and angulated body whorl.

***Reticharopa stenopleura*, new species. Plate 30, figs. 1–3.**

A species of *Reticharopa* in which the spiral ribs have been reduced on the body whorl and spire and the primary radial ribs are very close-set (73 on the body whorl).

Shell minute, solid, closely coiled, deeply and narrowly umbilicated, spire slightly elevated. Whorls 4 to  $4\frac{1}{8}$ , sharply rounded, body whorl descending in front. Sutures prominent, but not deeply channeled. Apical whorls  $1\frac{1}{2}$ , sculpture reticulated, spiral ribs less prominent than the radial (pl. 31, fig. 7). Body whorl and spire without prominent spiral ribs. Radial ribs prominent, close-set, slightly retractive. Secondary riblets present on and between the primaries. Aperture ovate, lip simple. Parietal callus thin, translucent. Umbilicus 0.4 mm.

wide, contained five times in the diameter. Diameter of holotype 2 mm., height 1.3 mm.

*Type*.—University of Michigan Museum of Zoology no. 186038. Collected from stream drift in the Sarakata River Valley, Espiritu Santo, New Hebrides (ML 95), by Robert E. Kuntz, May–June, 1944.

*Paratypes*.—UMMZ 186039 and BPBM 212377.

*Remarks*.—The reduced spiral ribbing of the post-apical whorls separates *R. stenopleura* from the other *Reticharopa*.

***Reticharopa* sp.** Plate 30, figs. 4–6.

*Range*.—Espiritu Santo.

*Material*.—ML 95.

*Remarks*.—A single specimen with depressed spire, broken apical whorls, and reticulated body sculpture probably represents another species of *Reticharopa*. The shell is flammulated with reddish-brown and white and is similar to the New Zealand species grouped in *Cavellia* (sens. lat.). Dell (1952a) showed that *Cavellia*, characterized by a depressed spire, is polyphyletic. Similarly, Iredale (1937a) placed the Austro-Tasmanian species with depressed spires in genera having the same apical sculpture rather than in a separate genus. Although the apical whorls of the New Hebridean specimen are missing, the spiral ribbing suggests that it is a *Reticharopa*.

***Reticharopa helva* (Cox).** Figure 3, *a–c*.

*Helix helva* Cox, 1870, Proc. Zool. Soc. London, 1870: 82—Aneiteum.

*Range*.—Aneiteum.

*Material*.—At 200 feet elevation, Aneiteum (DMNZ, W. H. Dawbin!). Photographs of holotype, courtesy of Australian Museum, Sydney).

*Remarks*.—The original description of *R. helva* failed to mention many of the systematically important characters, and even examination of the figures of the holotype furnished by Dr. Donald F. McMichael (fig. 3) did not enable me to classify this species satisfactorily. Fortunately, two partially broken specimens lent by the Dominion Museum identified *Helix helva* as a *Reticharopa*. The holotype (Australian Museum no. C. 62202) has the apical sculpture worn off and there is no spiral sculpture apparent on the post-apical whorls. It is 2.5 mm. in diameter and 1.3 mm. high, and has  $3\frac{3}{4}$  whorls. Both of the Aneiteum specimens from the Dominion Museum had worn apical whorls, but in one the umbilicus was free of obstruc-

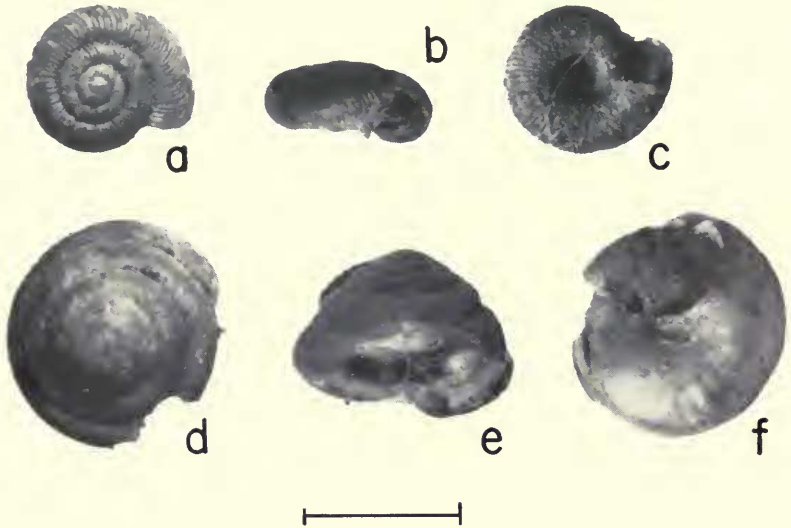


FIG. 3. *a-c*, *Reticharopa helva* (Cox) (photographs of holotype); *d-f*, *Helix ardua* Cox (= *Liardetia samoensis* (Mousson); photographs of holotype). Photographs courtesy of D. F. McMichael, Australian Museum, Sydney. Scale line=2 mm.

tions and examination of the under side of the embryonic whorls clearly revealed the reticulated pattern of *Reticharopa*. The one adult specimen has  $4\frac{3}{8}$  whorls and is 2.46 mm. in diameter and 1.36 mm. high. It has 106 major ribs on the last whorl.

One New Hebridean "*Charopa*" could not be identified. It has never been figured. The original description is reprinted below:

#### "*Charopa*" *perryi* Smith

*Charopa perryi* Smith, 1897, Ann. Mag. Nat. Hist., (6), 20: 520—Mota Island, New Hebrides, and Rotuma Island off the Fijis.

"Testa orbicularis, latissime umbilicata, alba, epidermide olivacea induta, lineis incrementi elevatis curvatis tenuibus instructa; spira depressa, supra anfr. ultimum paulo elata; anfractus quatuor, convexi, primus laevis, pellucidus, ultimus supra leviter declivis, antice subdescendens; apertura obliqua, irregulariter rotundata, intus alba; peristoma tenue, marginibus conniventibus, callo tenui albo junctis, columellari ad insertionem vix expanso. Diam. maj.  $3\frac{1}{2}$  millim., min. 3; alt. 2."

*Charopa perryi* was named after Mr. W. W. Perry, who collected it on Mota Island. Mota is a small "hat" island off Valua and Vanua Lava in the Banks Group. It is possible that *perryi* is not an endo-



dontid. It may be related to *Ouagapia radicalis* (Mousson) from Fiji. No material of *perryi* was available.

UMMZ 136770 (ex Walker, Ponsonby, Garrett) contains a single specimen that had been labeled *C. perryi*. This specimen is 6.3 mm. in diameter and has five whorls with a distinct shoulder on the body whorl. It is obviously misidentified and probably represents an undescribed species. Unfortunately, no locality data were given.

### Superfamily LIMACACEA

Marginal teeth with narrow, lengthened basal-plates, either unicuspid and thorn-like, or bicuspid by elevation of outer on middle cusp (Pilsbry, 1896, p. 110).

The three families, the Limacidae, Zonitidae, and Helicarionidae, are very closely related. The limacid slugs are easily characterized, but the differences between the Zonitidae and Helicarionidae are almost entirely anatomical. Shells of the two families cannot be separated unless the anatomy of the soft parts is known. Occasionally the zonitid subfamily, Vitrininae, is considered to be a fourth family intermediate between the Limacidae and Zonitidae (see Pilsbry, 1946b, p. 233). I have followed H. B. Baker (1941, p. 205) in recognizing the Zonitidae and Helicarionidae as distinct families, rather than Pilsbry, who included at least one helicarionid subfamily, the Euconulinae, in the Zonitidae, or Iredale (1939, et seq.), who divided the zonitoid snails into over a dozen families.

The Limacidae are Palearctic slugs. One genus, *Deroceras*, has spread into northern Asia and North America, and several others have been widely disseminated by commerce.

It is extremely difficult to determine the distribution of the other two families, since the anatomy of the Eurasian, African, and Neotropical "zonitoid" genera is imperfectly known. The Pacific Island species were very ably monographed by H. B. Baker (1938b, 1940, 1941). Melanesia was not included in the area covered by his study, but nearly all of the New Hebridean species belong to taxa represented in Polynesia. Because the characteristics and probable relationships of the supraspecific taxa have been summarized by Baker (loc. cit.), it was considered unnecessary to repeat them here. For convenience, however, diagnoses of the families Helicarionidae and Zonitidae have been included.

I saw fourteen species and subspecies of New Hebridean limacoid mollusks. One additional species, "*Helix*" *vannae-lavae* Cox (1870),

has never been figured and no material of it could be located. Specimens of two more species probably represent mislabeled lots. Of the fourteen species, eleven are endemic, two are widely distributed in the Pacific, and one is of uncertain status. I have described four species and one subspecies as new and have provided a single key for both families, since there are no obvious conchological characters separating them.

All the New Hebridean limacoids belong to the most primitive subfamilies. The zonitid subfamily Trochomorphinae has "the most endodontid shell in the entire Limacea" (Baker, 1941, pp. 269-270), and it shows affinities to the most primitive helicarionid subfamily, the Euconulinae, which, in turn, is closely related to the Microcystinae (Baker, 1938b, p. 11). The other helicarionid subfamily, the Sesarinae, is also considered primitive (Baker, 1941, pp. 238, 352). None of the advanced taxa of "zonitid" mollusks is represented in the New Hebrides.

In the genera for which anatomical material was available, *Dendrotrochus* and *Trochomorpha*, the New Hebridean species were found to belong to new sections or subgenera. Study of the animals of the endemic *Lamprocystis*, *Diastole*, and *Orpiella* will probably produce similar results. Without dissection of the soft parts, however, the infrageneric relationships of the endemic species cannot be determined with accuracy. Pending such studies, I have tentatively assigned the species to previously named subgeneric taxa.

Unlike most families of land Mollusca, the "zonitid" snails do not grow to a certain size and then cease addition of shell material. Growth is more or less continuous throughout the life of the individual and it is therefore impossible to assign an "adult" size to any species. For this reason, measurements comparing species are only valid when shells with the same numbers of whorls are used. Comparative measurements for the minute species are given in Table III. The measurements are not as detailed as those given by H. B. Baker (1938b, 1940, 1941), since most of the New Hebridean species are characterized by positive sculptural features or are representatives of widely distributed taxa. Both *Dendrotrochus* and *Trochomorpha* depart from the pattern shown by the minute species, since there is a partial thickening of the lip and columella and cessation of shell increment at about the same number of whorls. This may be a seasonal phenomenon. The morphometry of the New Hebridean *Dendrotrochus* and *Trochomorpha* is summarized in Tables IV-VI.

## Key to New Hebridean Limacacea

1. Shell large, more than 10 mm. in diameter . . . . . 2  
Shell small, less than 7 mm. in diameter . . . . . 7
2. Shell imperforate, or umbilicus contained more than eight times in the diameter . . . . . 3  
Umbilicus open, contained about five times in the diameter . . . . . 6
3. Umbilicus completely closed; lip thickened, slightly reflexed; shell without a suprapерipheral ridge . . . . . 4  
Umbilicus narrowly open; lip thin, not reflexed; shell with a prominent suprapерipheral ridge . . . . . *Inozonites bicarinata* (Semper)
4. Shell with less than six whorls; less than 15 mm. in height . . . . . 5  
Shell with  $6\frac{1}{8}$  or more whorls; more than 15 mm. in height.  
*Dendrotrachus layardi* (Hartman)
5. Shell solid; keeled (not carinate);  $5\frac{1}{4}$  whorls; Vate Island.  
*Dendrotrachus eva eva* (Pfeiffer)  
Shell thin; sharply carinate;  $5\frac{3}{4}$  whorls; Banks, Torres or Santa Cruz Islands.  
*Dendrotrachus eva stramineus* Sykes
6. Shell solid; color band, when present, not bordering the suture.  
*Trochomorpha bakeri*, new sp.  
Shell thin; color band, when present, bordering the suture.  
*Trochomorpha rubens* Hartman
7. Shell perforate or openly umbilicate . . . . . 9  
Shell with umbilicus completely closed . . . . . 8
8. Diameter at  $4\frac{5}{8}$  whorls 5.7 mm.; H/D ratio 0.54–0.61; Espiritu Santo.  
*Lamprocystis mendañae*, new sp.  
Diameter at  $4\frac{5}{8}$  whorls 4.3 mm.; H/D ratio 0.66–0.75; Vate and Aneiteum.  
*Lamprocystis guttula* (Pfeiffer)
9. Shell with spiral rib(s) on apex and/or spire . . . . . 10  
Shell smooth or with close-set radial ribs on spire . . . . . 12
10. Several spiral ribs on apex and spire . . . . . 11  
One spiral rib on spire, another on periphery of body whorl.  
*Coneuplecta (Conibycus) bicarinata*, new sp.
11. Shell minute (2.5 mm.); ribs continued on body whorl; base flat.  
*Coneuplecta (Sitalina) microconus* (Mousson)  
Shell large (4.8 mm.); ribs fading out on body whorl; base convex.  
*Diasole subcarinata*, new sp.
12. Shell smooth or with microscopic spiral or radial lines . . . . . 13  
Shell with fine radial ribs on spire, spiral lines on base.  
*Liardetia samoensis* (Mousson)
13. Shell large (4.5–6.0 mm.); no spiral sculpture . . . . . 14  
Shell minute (2 mm.); microscopic spiral lines . . . . . *Wilhelminaia* sp.
14. Shell relatively depressed; Espiritu Santo.  
*Orpiella (?Halozonites) retardata depressa*, new subsp.  
Shell more elevated; Vate, Aneiteum . . . *Orpiella (?Halozonites) retardata* (Cox)

## Family HELICARIONIDAE

Primitively with tripartite sole, well-developed caudal foss overhung by "horn" and multicuspid radular marginals, all of which are usually accentuated or reverted to when shell is reduced; advanced groups with well-developed amatorial organs or dart-apparatus on female side of genitalia; shell rarely umbilicate and with perforation or rimation often closed by internal callus (H. B. Baker, 1941, p. 205).

The subfamily Microcystinae is endemic to the Pacific islands, but most of the other subfamilies are continental groups. The Euconulinae is the most primitive, but it is very closely related to the Microcystinae. The third subfamily found in the New Hebrides, the Sesarinae, has a discontinuous distribution probably resulting from replacement by more advanced helicarionids on continental areas. The characteristics allying and separating the various subfamilies of the Helicarionidae are given by Baker (1941, pp. 208-209).

### Subfamily EUCONULINAE

Of the three New Hebridean species of Euconulinae, one, *Coneuplecta* (*Conibycus*) *bicarinata*, is endemic, another, *Coneuplecta* (*Sitalina*) *microconus* (Mousson), is widely dispersed in the Pacific, and the third, *Wilhelminaia* sp., has uncertain status. Discussions of the systematic position and content of the Euconulinae are given by Baker (1941, pp. 212-213) and Pilsbry (1946b, pp. 233-234).

### Genus WILHELMINAIA Preston, 1913

Shell corneous, turbinate, perforate, sculptured throughout with very fine, spiral, punctate striae (Preston, 1913, p. 434).

*Type species.*—*Wilhelminaia mathildae* Preston.

*Remarks.*—The status of the species included in *Wilhelminaia* is very uncertain. Usually they are placed in "*Microcystis*" or "*Microcystina*," catch-all taxa for small to minute Indo-Pacific zonitids. H. B. Baker (1938b, p. 57) restricted *Microcystis* to some species from the Austral and Cook Islands. *Microcystina*, described from the Nicobar Islands and subsequently enlarged to include many Indonesian species (see B. Rensch, 1932, and van Benthem Jutting, 1950), has a much larger shell and different radular and genital structure than the only *Wilhelminaia* whose anatomy has been figured (see H. B. Baker, 1941, p. 227, pl. 44, figs. 1, 2). *W. minuscula* Preston, a manuscript species of Preston's from Batjan Island, "*Microcystina*" *gratilla* van Benthem Jutting (1950, pp. 448-450, figs. 68-69), the Caroline Island specimens reported by H. B. Baker (1941, pp. 226-227), the genotype, and the Melanesian specimens I have seen during this study I have temporarily grouped as a generic unit. *Discoconulus sinapidium* (Reinhardt) from Harima, Japan (UMMZ 147956, ex Walker, Ponsonby, Gude, Hirase), is similar but has weaker apical sculpture and differently shaped radular teeth.

*W. mathildae* has never been figured, and I could not locate any specimens. Shells of *W. minuscula* Preston and the Batjan species

Table III.—Measurements of the New Hebridean Limacacea

| Species                             | Greater diameter | Lesser diameter | Height | H/D  | Whorls |
|-------------------------------------|------------------|-----------------|--------|------|--------|
| <i>Wilhelminaia</i> sp.             |                  |                 |        |      |        |
| Florida Island, Solomons            |                  |                 |        |      |        |
| (FLW 40).....                       | 1.62             | 1.49            | 0.92   | 0.57 | 3½     |
|                                     | 1.49             | 1.39            | 0.92   | 0.58 | 3½     |
|                                     | 1.52             | 1.42            | 0.99   | 0.65 | 3½     |
| (FLW 38).....                       | 1.88             | 1.72            | 1.19   | 0.63 | 4½     |
|                                     | 1.72             | 1.55            | 1.06   | 0.62 | 3¾     |
|                                     | 1.91             | 1.73            | 1.19   | 0.62 | 4¼     |
|                                     | 1.65             | 1.52            | 0.99   | 0.60 | 3⅝     |
| New Hebrides (ML 39)...             | 1.88             | 1.75            | 1.19   | 0.63 | 4½     |
| (ML 35).....                        | 1.65             | 1.52            | 1.06   | 0.64 | 3⅝     |
|                                     | 1.72             | 1.62            | 1.12   | 0.65 | 3¾     |
| (ML 95).....                        | 1.85             | 1.72            | 1.16   | 0.63 | 4      |
|                                     | 1.78             | 1.65            | 1.12   | 0.63 | 3⅞     |
| Batjan Island, Moluccas             |                  |                 |        |      |        |
| (UMMZ 148388).....                  | 1.58             | 1.48            | 0.99   | 0.63 | 3½     |
|                                     | 1.58             | 1.45            | 0.99   | 0.63 | 3½     |
| <i>Liardetia samoensis</i>          |                  |                 |        |      |        |
| (ML 95).....                        | 3.14             | 2.98            | 2.38   | 0.76 | 4⅞     |
| <i>Coneuplecta microconus</i> ..... |                  |                 |        |      |        |
| (ML 95).....                        | 2.68             | 2.54            | 2.24   | 0.84 | 5½     |
|                                     | 2.61             | 2.44            | 2.48   | 0.95 | 5¾     |
| <i>C. bicarinata</i> , type.....    | 2.44             | 2.31            | 2.14   | 0.88 | 4½     |
| <i>Lamprocystis guttula</i>         |                  |                 |        |      |        |
| (Miller 598).....                   | 4.4              | 4.1             | 3.3    | 0.75 | 5      |
|                                     | 4.3              | 4.0             | 2.9    | 0.68 | 4⅝     |
|                                     | 3.4              | 3.1             | 2.2    | 0.65 | 3⅞     |
| UMMZ 147868.....                    | 5.0              | 4.6             | 3.7    | 0.74 | 5      |
| Aneiteum (AMNH).....                | 3.3              | 3.0             | 2.2    | 0.67 | 4½     |
| <i>L. mendañaë</i> , holotype.....  |                  |                 |        |      |        |
| paratypes.....                      | 5.8              | 5.4             | 3.4    | 0.59 | 4⅝     |
|                                     | 4.7              | 4.4             | 2.8    | 0.60 | 3⅝     |
|                                     | 4.8              | 4.4             | 2.9    | 0.60 | 3⅞     |
| CNHM 55197, paratype..              | 5.7              | 5.3             | 3.1    | 0.54 | 4⅞     |
| <i>Diastole subcarinata</i> .....   |                  |                 |        |      |        |
|                                     | 4.8              | 4.4             | 3.2    | 0.67 | 4¼     |
|                                     | 4.8              | 4.4             | 3.2    | 0.67 | 4¼     |
| holotype.....                       | 4.8              | 4.4             | 3.3    | 0.69 | 4¼     |
| <i>Orpiella retardata</i> .....     |                  |                 |        |      |        |
|                                     | 4.5              | 4.0             | 2.5    | 0.56 | 4½     |
|                                     | 5.0              | 4.6             | 3.2    | 0.64 | 4¾     |
| <i>O. r. depressa</i> , type.....   |                  |                 |        |      |        |
|                                     | 5.1              | 4.5             | 2.7    | 0.53 | 4⅝     |
|                                     | 5.9              | 4.6             | 3.3    | 0.54 | 5      |

(UMMZ) were very similar to the Melanesian shells. H. B. Baker (1941, pp. 226-228) referred some Caroline Island specimens to *Discoconulus* and compared them to *sinapidium*. He had not seen any specimens of *Wilhelminaia*. His description and figure of one specimen (op. cit., p. 227, pl. 60, fig. 14) match the specimens of *Wilhelminaia* better than those of *Discoconulus sinapidium*. Dr. Y. Kondo compared the New Hebridean and Caroline Island shells without discovering any differences.

**Wilhelminaia** sp. (? *mathildae* Preston). Plate 33, figs. 1-3.

*Range*.—Espiritu Santo, Florida Island, Solomon Islands, Caroline Islands, and Indonesia.

*Material*.—ML 35, ML 39, ML 44, ML 74, ML 95; New Hebrides (UMMZ, ex Walker, Ponsonby); Florida Island, Solomon Islands (UMMZ, ex Kuntz!); Batjan Island, Moluccas (UMMZ 148386, UMMZ 148387, and UMMZ 148388, ex Walker, Preston).

*Remarks*.—The Indonesian specimens cited above were under a manuscript name of Preston's and their identification with *W. mathildae* is uncertain. Certainly there were no important differences between the Indonesian and Melanesian specimens that I examined during this study. I suspect that only one wide-ranging species of *Wilhelminaia* will eventually be recognized.

Genus **CONEUPLECTA** Moellendorff, 1893

*Coneuplecta microconus* (Mousson) and *C. calculosa* (Gould) have been widely distributed in the Pacific by human agency (H. B. Baker, 1941, p. 235). *Coneuplecta* is common in the Philippines and Indonesia, but only the two species mentioned above reach Polynesia. H. B. Baker (op. cit., pp. 232-233), with some hesitation, included a number of genera described by Thiele and Iredale in the synonymy of *Coneuplecta*. One New Hebridean species, *C. bicarinata*, new species, seems referable to *Conibycus* (Thiele, 1928a, p. 135). Pending study of the soft parts, I have retained *Conibycus* as a subgenus of *Coneuplecta*, although it may prove to be a separate genus. *Coneuplecta microconus* is widely distributed in the New Hebrides, but *C. calculosa* has not yet been found there.

**Coneuplecta (Sitalina) microconus** (Mousson). Plate 34, fig. 10.

*Nanina microconus* Mousson, 1865, Jour. de Conch., 13: 192—Lomma-Lomma, Fiji Islands.

*Helix sansitus* Cox, 1870, Proc. Zool. Soc. London, 1870: 83—Viti Levu, Fiji, and Vanua Lava, Banks Islands.

*Trochonanina microconus* (Mousson), Garrett, 1887, op. cit., 1887: 172—Tonga and Samoa.

*Sitala sansitus* (Cox), Gude, 1913, Proc. Malac. Soc. London, 10: 328, pl. 14, fig. 7a-c—Suva Harbor, Fiji Islands.

*Coneuplecta (Sitalina) microconus* (Mousson), Baker, 1941, Bull. B. P. Bishop Mus., 166: 236-237, pl. 55, fig. 6.

*Range*.—Espiritu Santo, Aneiteum, Vate, and Vanua Lava. Fiji, Samoa, and Tonga.

*Material*.—ML 26a, ML 31a, ML 50, ML 63, ML 66, ML 70, ML 76a, ML 95; New Hebrides (UMMZ 161077, ex Walker, Ponsonby); Vila, Vate (Australian Museum, A. R. McCulloch!); Aneiteum (DMNZ, W. H. Dawbin!); numerous lots from Polynesia.

*Remarks*.—The New Hebridean specimens are not separable from the Fijian "*sansitus*" studied by Gude (loc. cit.) (UMMZ 148445 and CNHM 43411). I have therefore synonymized "*Helix*" *sansitus* despite the fact that I have not re-examined the types.

***Coneuplecta (Conibycus) bicarinata***, new species. Plate 33, figs. 7–9.

A species of *Conibycus* easily separated from *C. dahl*i Thiele and *C. aruensis* Thiele by having a supra-medial thread-like carina on the spire and a second carina on the periphery of the body whorl.

Shell trochoidal, apex slightly depressed, whorls  $4\frac{1}{2}$  to  $4\frac{3}{4}$ , regularly and gradually increasing in size. Sutures impressed, whorls rounded. Aperture obliquely ovate. Umbilicus barely perforate, basal lip reflected over and partially covering perforation. Sculpture of many fine spiral threads, crossing low, irregular growth wrinkles. One thread, slightly above the middle of the whorl, greatly enlarged, forming a distinct carina on the spire. A second carina on periphery of body whorl. Diameter of holotype 2.44 mm., height 2.14 mm., with  $4\frac{1}{2}$  whorls.

*Type*.—University of Michigan Museum of Zoology no. 186108. Collected from stream drift in the Sarakata River Valley, Espiritu Santo (ML 95), by Robert E. Kuntz, May–June, 1944.

*Paratype*.—A single paratopotype is BPBM 212375.

*Remarks*.—Only two specimens, one broken, of *C. bicarinata* were available. The basic sculpture is typical of *Coneuplecta*, but the thread-like carinae at once separate *bicarinata* from any Pacific species. An extremely similar shell, "*Sitala*" *subbilitata* Godwin-Austen, is found in the Andaman Islands. Specimens of *subbilitata* (UMMZ 148446, ex Walker, Godwin-Austen) have the identical sculpture of threads and carinae found in *bicarinata*. *C. bicarinata* differs from *subbilitata*, however, in having a much narrower umbilicus and a more elevated spire. The relationship of the Indian and Indonesian *Sitala* to *Coneuplecta* remains to be determined. Without study of the soft parts it will be impossible to decide whether *bicarinata* and *subbilitata* represent convergent species in unrelated genera or parallel developments from the same ancestral stock (?*Conibycus* from Papua). On the basis of other taxa, I consider that the latter possibility is probably correct.

The nearest relatives of *C. bicarinata* in the Pacific seem to be *C. dahli* from New Britain and *C. aruensis* from the Aru Islands (Thiele, 1928a, p. 137, pl. 5, figs. 26-27). Both species have the apex of the spire slightly, though distinctly depressed. Typical *Coneuplecta* has the apical whorls at the same angle as the rest of the spire.

### Subfamily MICROCYSTINAE

If broad interpretations of subfamilial categories are utilized, the Microcystinae can be merged with the Euconulinae into one subfamily. Following H. B. Baker (1941, pp. 208-209), I have adopted the narrower subfamily units. Three of the four microcystine species found in the New Hebrides, *Lamprocystis guttula* (Pfeiffer), *L. mendañae*, new sp., and *Diastole subcarinata*, new sp., are endemic; the fourth, *Liardetia samoensis* (Mousson) (= *striolata* Pease), is widely distributed in the Pacific.

#### Genus LIARDETIA Gude, 1913

The only endemic Polynesian species of *Liardetia* are found in the Society Islands. Two species, *L. discordiae* (Garrett) and *L. samoensis* (Mousson), appear to have been widely disseminated. It seems probable that the center of distribution lies in Indonesia, since by far the greatest number of species are found there (van Benthem Jutting, 1950, pp. 393-412). The New Hebridean species, *L. samoensis*, has the widest range of any species.

#### *Liardetia* (*Liardetia*) *samoensis* (Mousson). Figure 3, *d-f*; Plate 33, figs. 4-6.

*Nanina samoensis* Mousson, 1865, Jour. de Conch., **13**: 165—Upolu, Samoa.

*Helix ardua* Cox, 1870, Proc. Zool. Soc. London, **1870**: 82—Erromanga, New Hebrides (Brazier!).

*Helix antelata* Cox, 1870, op. cit., pp. 83-84—Aneiteum, New Hebrides (Brazier!).

*Guppya papuana* Thiele, 1928, Zool. Jahrb., Syst., **55**: 113, pl. 5, fig. 20—Ralum, New Britain.

*Liardetia* (*Liardetia*) *striolata* (Pease), Baker, 1938, Bull. B. P. Bishop Mus., **158**: 22-24, pl. 9, figs. 5, 6; pl. 14, fig. 12.

*Liardetia* (*Liardetia*) *samoensis* (Mousson), Baker, 1940, op. cit., **165**: 190—correction of name, since *striolata* is preoccupied.

*Range*.—Espiritu Santo, Aneiteum, and Erromanga. New Caledonia, Solomons, Bismarcks, Marshalls, Ellices, Fiji, Samoa, Cook, Society, and Marquesas.



*Material*.—ML 50, ML 63, ML 69, ML 95; Aneiteum (UMMZ, ex Australian Museum, paratypes of *Helix antelata* Cox); Erromanga (UMMZ, ex Australian Museum); New Hebrides (UMMZ 162016, ex Walker, Ponsonby); Bourail, New Caledonia (UMMZ); many Polynesian specimens.

*Remarks*.—*Liardetia samoensis* varies greatly in size and shape. Juvenile shells have a low spire and correspond to the form called *antelata* Cox; gerontic individuals have a very high spire and represent the form *ardua* Cox (fig. 3). Specimens matching both extremes, as well as numerous intermediate individuals, were found on Espiritu Santo. Franc (1957, p. 147) reports this species from New Caledonia as *Kaliella subfulva* (Gassies).

#### Genus **DIASTOLE** Gude, 1913

The nomenclatural confusion necessitating the replacement of *Trochonanina* of authors by *Diastole* Gude was summarized by H. B. Baker (1938b, pp. 45–46). *Diastole* is primarily a Polynesian genus, with species found in the New Hebrides and Fijis. Study of the Papuan and Indonesian “zonitids” may result in a great westward extension of its range. The New Hebridean *Diastole subcarinata*, new sp., is somewhat intermediate between *Diastole* (sens. str.) and *Trochonanita* Baker, 1941. It has the scarcely beaded spiral ridges and no columellar fold of the former, but the number of major spiral ridges of the latter. *D. subcarinata* is characterized by its small size, weak carina, and lack of a columellar fold.

#### **Diastole (Diastole) subcarinata**, new species. Plate 32, figs. 4–6.

A species of *Diastole* most closely related to the Society Island *D. necrodes* Baker but easily separated by virtue of its smaller size, less acute carina, and lack of a columellar lamella.

Shell depressed trochoidal, body whorl angulated with a thin epidermal carina, whorls slowly and gradually increasing in size. Base of shell slightly flattened laterally, sutures impressed, whorls of spire gently and evenly rounded. Holotype very light horn-colored, paratypes bleached. Whorls  $4\frac{1}{4}$ , embryonic ones (pl. 32, fig. 6) with eleven spiral ridges, faintly beaded by radial lines. Ridges becoming less prominent on spire, almost completely lacking on body whorl. Growth wrinkles becoming more prominent on later whorls. Base of shell with only faint traces of sculpture. Aperture compressed, basal margin paralleling contour of penultimate whorl, distinctly angulate at periphery. Columella slightly thickened, but without trace of a lamella. Diameter of holotype 4.8 mm., height 3.3 mm.

*Type*.—University of Michigan Museum of Zoology no. 186103. Collected from stream drift in the Sarakata River Valley, Espiritu

Santo, New Hebrides (ML 95), by Robert E. Kuntz, May–June, 1944.

*Paratypes*.—Paratopotypes are UMMZ 186102, BPBM 212372.

*Remarks*.—With the exception of *D. lamellaxis* Baker, *D. subcarinata* is the smallest member of the genus known. *D. subcarinata* differs from *D. lamellaxis* in being much less sharply carinate and more depressed. Only three specimens of *D. subcarinata* were available.

### Genus **LAMPROCYSTIS** Pfeiffer, 1883

H. B. Baker (1938b, pp. 68–92) monographed the Polynesian and Micronesian species of *Lamprocystis*. Some Indonesian species have been referred to the genus (see van Benthem Jutting, 1950), but the western limits of distribution are unknown. No preserved specimens of the New Hebridean species were available. On the basis of conchological characters, both *Lamprocystis guttula* (Pfeiffer) and *L. mendañae*, new sp., belong to *Lamprocystis* (sens. str.). They differ from the Fijian and Samoan species in having the columellar lamellae reduced and more elevated; from the Mariana *L. denticulata* (Quadras and Moellendorff) they are distinguished by having the columellar lamellae higher and less prominent.

### **Lamprocystis (Lamprocystis) guttula** (Pfeiffer). Plate 34, figs. 11, 12.

*Helix guttula* Pfeiffer, 1853 (March), Zeits. f. Malak., **10**, (4), p. 53—New Zealand (error); Reeve, 1853 (May), Conch. Icon., *Helix*, pl. 158, fig. 1040—New Zealand (error); Pfeiffer, 1854, Proc. Zool. Soc. London, **1853**: 58—New Zealand (error); Pfeiffer, 1859, Monog. Helic. viv., **4**: 15.

*Hyalina (Conulus) layardi* Thomson, 1885, Proc. Zool. Soc. London, **1885**: 26–27, figs.—Vate Island, New Hebrides.

*Microcystis guttula* (Gould) (sic), Sykes, 1903, Proc. Malac. Soc. London, **5**: 196—Port Vila, Vate Island.

*Lamprocystis layardi* (Thomson), Ancey, 1905, Nautilus, **19**, (4), p. 42—Vate (Glisson!).

*Lamprocystis (Lamprocystis) excrescens* (Mousson), Baker, 1938, Bull. B. P. Bishop Mus., **158**: 85—(part).

*Range*.—Vate and Aneiteum.

*Material*.—Vila, Vate (Miller 598); Vate (UMMZ 147868, ex Walker, Ponsonby, Layard, paratypes of *layardi* Thomson; CNHM 43041, ex Webb, Gude, paratype of *layardi* Thomson); Aneiteum (AMNH, Macmillan!, 1937); New Hebrides (UMMZ 147867, ex Walker, Ponsonby, Garrett).

*Remarks.*—The identity of *Helix guttula* Pfeiffer has long been uncertain. Sykes (1903) united *layardi* and *guttula*. Specimens from the British Museum (CM 62.29194), which are the *excrescens* of H. B. Baker (1938b, pl. 13, figs. 5, 6) are labeled *guttula*. The specimen figured in the *Conchologia Iconica* clearly shows the high spire and single columellar "tooth" of the Vate shells, rather than the characters of the true *excrescens*, as emphasized by Ancey (1905, p. 42). Evidence that *Helix guttula* is a mislabeled New Hebridean shell is provided by *Delos (Hebridelos) rapida* (Pfeiffer), which was described from "New Zealand" at the same time and is now known to be New Hebridean.

*L. guttula* differs from *L. excrescens* in lacking basal teeth in young shells, in having a shorter columellar lamella, and in being much more trochoidal. *L. mendañae* has the same columellar structure as *L. guttula*, but is more depressed and slightly larger.

**Lamprocystis (Lamprocystis) mendañae**, new species. Plate 34, figs. 7-9.

*Nanina (Microcystis) excrescens* Mabille (not Mousson), 1895, Bull. Soc. d'hist. nat. d'Autun, 8: 109—New Hebrides (François!).

A species of *Lamprocystis* characterized by its large size (5.8 mm. at 4½ whorls), low spire, angulated body whorl, and small columellar lamella.

Shell broadly conoid, depressed, imperforate; body whorl slightly angulated on adults (3½ whorls), more sharply angulated on juveniles. Surface smooth, shining, with only slight suggestion of spiral striae. Suture broadly overriding, only slightly impressed. Aperture with rounded periphery, small, not flaring. Lip thin, slightly thickened and reflexed basally. Columella with a small, rounded spiral lamella, more prominent and sharply delimited in young shells. Color very light horn. Diameter of holotype 5.8 mm., height 3.4 mm., with 4½ whorls.

*Type.*—University of Michigan Museum of Zoology no. 181741. Collected from river drift in the Sarakata River Valley, Espiritu Santo, New Hebrides (ML 95), by Robert E. Kuntz, May-June, 1944.

*Paratypes.*—On Espiritu Santo, specimens were collected at ML 69 and ML 95 (type locality). Paratypes are UMMZ 181740, UMMZ 186100, CNHM 55197, BPBM 212373, ANSP, MCZ.

*Remarks.*—In columellar structure *L. mendañae* is almost identical with *L. guttula*, but the smaller size and relatively higher spire of the latter easily separate the two species. As in most zonitids, there is considerable difference in shape between old and young specimens. *L. mendañae* is named after the Spanish explorer, Alvaro de Mendaña.

Subfamily **SESARINAE**

The Sesarinae are rather primitive helicarionids which have a discontinuous distribution. Although diverse in shell structure, anatomical similarities indicate that the Sesarinae are a natural assemblage. Two genera, *Orpiella* and *Dendrotrochus*, yielded interesting information on the affinities of the New Hebridean species.

Genus **ORPIELLA** Gray, 1855

Only the Fijian species of *Orpiella* have been adequately studied for anatomical characters and conchological variation. Numerous "species" are known from the Solomons, Bismarcks, and New Guinea, but their relationship to the Fijian taxa cannot be determined without more study (H. B. Baker, 1941, p. 352). The two New Hebridean morphs appear to be most similar to the Fijian group that H. B. Baker (1941, pp. 240-243) placed in *Halozonites* Pilsbry and Cooke, 1941. Pending study of the animals, I have tentatively referred *O. retardata* and *O. retardata depressa* to *Halozonites*. The only difference between *retardata* and *depressa* is that the latter is less elevated. I consider them to be only subspecifically distinct.

**Orpiella (?Halozonites) retardata retardata** (Cox). Plate 34, figs. 1-3.

*Helix retardata* Cox, 1870, Proc. Zool. Soc. London, 1870: 84—Aneiteum (Brazier).

*Macrochlamys* (?) *annatonensis* Ancy (not Pfeiffer), 1905, Nautilus, 19, (4), p. 42—Vate (Glisson).

*Range*.—Vate, Aneiteum.

*Material*.—Vila, Vate (Miller 598; USNM 598360 ex Miller; UMMZ 147918 ex Walker, Ponsonby, Ancy, Layard); Vate (UMMZ 162021 ex Walker, Ponsonby, Layard); Aneiteum (UMMZ ex Australian Museum, paratypes of *Helix retardata* Cox).

*Remarks*.—The paratypes of *Helix retardata* are very young individuals and quite different in appearance from typical adults. Kobelt placed *retardata* in the rhytidid genus *Macrocycloides*, but examination of the paratypes does not support this.

*O. retardata* differs from *Orpiella* of similar size by its narrow umbilicus and angulated body whorl.

**Orpiella (?Halozonites) retardata depressa**, new subspecies. Plate 34, figs. 4-6.

A subspecies of *Orpiella retardata* which differs from the nominate form only by having a more depressed spire.

Sculpture, umbilicus, aperture, color, and whorl increase as in typical *retardata*. Spire more depressed and shells larger in diameter than specimens of the nominate form with the same number of whorls. Diameter of holotype 5.1 mm., height 3.0 mm., with  $4\frac{5}{8}$  whorls.

*Type*.—University of Michigan Museum of Zoology no. 186112. Collected in the jungle between the Renee and Sarakata Rivers, Espiritu Santo, New Hebrides (ML 26b), by Robert E. Kuntz on January 20, 1944.

*Paratypes*.—On Espiritu Santo, Kuntz collected this subspecies from ML 26b (type locality), ML 33, ML 39, ML 74, ML 95. Paratypes are UMMZ 186109, UMMZ 186110, UMMZ 186113, BPBM 212371, CNHM, MCZ, ANSP, and USNM.

*Remarks*.—Comparisons of the 57 specimens of *O. r. depressa* with the 19 specimens of *O. r. retardata* failed to reveal any characters, other than height and diameter, by which the two can be separated. Most individuals could be easily placed in one subspecies or the other, but a few intergrading shells were seen. Despite the geographic isolation, *retardata* and *depressa* are probably only subspecifically separable.

#### Genus DENDROTRUCHUS Pilsbry, 1894

(= *Trochonanina* Rensch, 1930 et seq., not Mousson, 1869)

For many years both the systematic and the nomenclatural status of *Dendrotrochus* were uncertain. On the basis of conchological similarity, Pilsbry established *Dendrotrochus* as a section of the camaenid genus *Papuina*. Hedley (1895a) dissected the animals and placed *Dendrotrochus* near *Trochomorpha*. Convergence in shell structure led I. & B. Rensch to combine *Dendrotrochus* with the microcystine genus *Diastole* (= *Trochonanina* Garrett, Rensch, etc., not Mousson, 1869). H. B. Baker (1941, p. 256) placed *Dendrotrochus* in the Sesariinae after dissecting several species. His classification is followed here.

The exact range of *Dendrotrochus* is uncertain. It is definitely known from the New Hebrides, Santa Cruz, Solomons, Bismarcks, Admiralty and Caroline Islands (fig. 19), but anatomical investigations may prove that some of the New Guinean and Australian "*Papuina*" are congeneric.

I. Rensch (1934b, 1937) reviewed the species of *Dendrotrochus*, but the taxonomic status of the numerous morphs remains uncertain. The shells vary greatly in size, color, elevation and degree of carination. Apparently there are terrestrial and arboreal species, since both types of radulae are found (I. Rensch, 1934b, pp. 3, 23). Par-

ticularly in respect to the taxa of northern Melanesia, no satisfactory conclusions can be drawn as to the type and extent of speciation.

Only a few species have been dissected. They agree in the general facies of the genitalia, jaw, mantle lappets, and caudal areas, but show a remarkable series of divergences in the internal structure of the penis. The Caroline Island species was placed in a new subgenus, *Ponapea*, by Baker (1941, p. 256), because it lacked a utricule surrounding the verge. Typical *Dendrotrochus* is found in the Solomons, and I dissected one species, *D. cleryi cleryi* (Recluz), for comparison with the New Hebridean *D. layardi* (Hartman). The external features of the genitalia are quite similar, but the internal structures of the penis (pl. 23, figs. 1-4) are quite different. The New Hebridean species has two large pilasters flanking the verge and a large ovoid stimulator in a sac to one side of the atrium, but all of these are lacking in *D. cleryi*. On the basis of the penial structure, *D. layardi* is herein made the type of a new subgenus, *Santotrochus*. Specimens of *D. eva* from Vate (BM loan in 1958) have the same structures as *D. layardi*.

#### SANTOTROCHUS, new subgenus

Male genitalia with a verge flanked by two pilasters and a large, flat stimulator at one side of the atrium. Female genitalia and shell as in the typical subgenus.

*Type species.*—*Oxychona layardi* Hartman.

*Remarks.*—Two species of *Dendrotrochus* are known from the New Hebrides. *D. layardi* is restricted to Espiritu Santo and *D. eva* (Pfeiffer) apparently is found on Vate, Epi, the Banks, Torres, and Santa Cruz Islands. *D. eva eva* lives on Vate and Epi; the northern islands have a weakly differentiated race, *stramineus* Sykes. A third species, *D. cyrene* (Crosse) (see Jour. de Conch., 17: 183-184; 18: 102-103, pl. 2, fig. 2), from an unknown locality, may be from the New Hebrides. It is equally possible, however, that it may have come from the Solomons. The unique holotype of *D. cyrene* is in the collection of the Journal de Conchyliologie in Paris. "*Helix*" *jenynsi* Pfeiffer, described without locality, was reported from Tanna by Reeve (Conch. Icon., *Helix*, pl. 150, fig. 979). The figured shell may be a young *Dendrotrochus*, but the correctness of the locality is questionable.

***Dendrotrochus* (*Santotrochus*) *eva eva* (Pfeiffer).** Plate 10, fig. 13; plate 25, figs. 1, 2.

*Helix eva* Pfeiffer in Reeve, 1853, Conch. Icon., *Helix*, pl. 150, fig. 977—Solomon Islands (error); Pfeiffer, 1854, Proc. Zool. Soc. London, 1852: 84—

New Hebrides; Pfeiffer, 1854, *Conch. Cab.*, I, 12, (3), p. 490, pl. 160, figs. 22-23—New Hebrides; Brazier, 1880, *Jour. de Conchy.*, 28: 313-314—Vate.

*Helix (Papuina) eva* Pfeiffer, Pilsbry, 1891, *Man. Conch.*, (2), 7: 78-79, pl. 15, figs. 76-78, 84-85, pl. 16, figs. 1-4—Vate.

*Dendrotrochus eva* (Pfeiffer), Pilsbry, 1894, *Man. Conch.*, (2), 9: 143; Sykes, 1903, *Proc. Malac. Soc. London*, 5: 196—Port Vila, Vate (J. J. Walker); Ancey, 1905, *Nautilus*, 19, (4), p. 43—Vate.

*Range*.—Vate Island and Epi Island.

*Material*.—Vila, Vate (USNM 598363 ex Miller; Miller 538; ANSP 133298 ex Froggatt); Vate (UMMZ 76488 ex Walker, Ponsonby, Willey; UMMZ 76485 ex Walker, Ponsonby; ANSP 48922 ex Depuy; MCZ 8656 ex Winkley; MCZ ex Beddome; CM 62.4491 ex Hartman; CM 62.13644 ex Clapp, Hartman; CNHM ex Webb, Gude, Layard); Nivenue, Epi, at 900 feet elevation (DMNZ, A. G. Horwell!); New Hebrides (ANSP 1912 ex Brown, Cuming, Cox; UMMZ 11931 ex Stearns; UMMZ 76484 ex Walker, Ponsonby, Wetherby, Garrett; AMNH 61730; AMNH 38397 ex Crooke; MCZ ex Grand Rapids Museum; MCZ ex Pease; MCZ 133876 ex Putzeys; MCZ ex Cox; MCZ 102842 ex Bequaert).

*Remarks*.—At least two recognizably different races of *D. eva* are found on Vate, only one of which can be accurately localized. Shells from near Vila correspond perfectly to the holotype (pl. 10, fig. 13). The type locality is here restricted to the vicinity of Port Vila. The Port Vila shells are keeled, not carinate, appreciably higher, and with more whorls than are found in the northern race, *stramineus* (see Table IV). Vate Island specimens distributed by Layard, however, are intermediate between *eva* and *stramineus* in respect to whorl count ( $5\frac{3}{8}$  to  $5\frac{1}{2}$  whorls), coloration, and degree of carination. It is probable that the shells were collected at Seaview and Rathmor plantations, the locations of which I was unable to discover. Possibly other morphological forms will be found when Vate has been more thoroughly explored. The Epi Island specimens show a range of variation encompassing both the Vate Island morphotypes.

***Dendrotrochus (Santotrochus) eva stramineus* Sykes.** Plate 10, fig. 14; plate 25, figs. 3-5.

*Dendrotrochus stramineus* Sykes, 1903, *Proc. Malac. Soc. London*, 5: 196-197, fig. 1—Lo, Torres Islands and Vanua Lava, Banks Islands (type locality) (J. J. Walker).

*Range*.—Torres, Banks, and Santa Cruz Islands.

Table IV.—Size Variation in the New Hebridean *Dendrotrochus*

|  |       | Diameter  | Height    | H/D       | Whorls                           |
|--|-------|-----------|-----------|-----------|----------------------------------|
| <i>D. eva eva</i> . . . . .<br>Vila, Vate<br>(17 specimens)              | Mean  | 13.8      | 10.4      | 0.74      | 5 $\frac{3}{4}$                  |
|  | Range | 13.1–15.0 | 9.3–11.2  | 0.63–0.82 | 5 $\frac{1}{2}$ –6               |
|  | S.D.  | 0.66      | 0.53      | 0.048     | ...                              |
| <i>D. eva eva</i> . . . . .<br>Nivenue, Epi<br>(7 specimens)             | Mean  | 14.0      | 10.0      | 0.72      | 5 $\frac{3}{4}$                  |
|  | Range | 13.1–14.8 | 9.1–10.9  | 0.64–0.79 | 5 $\frac{1}{2}$ –5 $\frac{7}{8}$ |
|  | S.D.  | 0.85      | 0.65      | 0.057     | ...                              |
| <i>D. e. stramineus</i> . . . . .<br>Santa Cruz Island<br>(20 specimens) | Mean  | 13.8      | 9.2       | 0.67      | 5 $\frac{1}{8}$                  |
|  | Range | 12.6–15.0 | 8.5–10.1  | 0.61–0.71 | 5–5 $\frac{7}{8}$                |
|  | S.D.  | 0.73      | 0.48      | 0.037     | ...                              |
| <i>D. layardi</i> . . . . .<br>Espiritu Santo<br>(37 specimens)          | Mean  | 16.6      | 14.4      | 0.87      | 6 $\frac{5}{8}$                  |
|  | Range | 15.3–18.0 | 12.7–16.6 | 0.76–0.98 | 6 $\frac{1}{8}$ –7 $\frac{1}{4}$ |
|  | S.D.  | 0.76      | 0.61      | 0.062     | ...                              |

*Material*.—Graciosa Bay, Santa Cruz Island (MCZ 192354 ex A. G. Stevenson, C. E. Fox); Santa Cruz Island (AMNH 73353, W. M. Mann; UMMZ 182858 ex MCZ, W. M. Mann; MCZ 32476, MCZ 32477, MCZ 32478, MCZ 32479, all W. M. Mann; UMMZ 76487 ex Walker, Ponsonby); Banks Islands (MCZ 108715 ex P. Dautzenberg); photograph of holotype (courtesy of BM).

*Remarks*.—The Port Vila and Santa Cruz Island specimens are usually separable on the basis of color and degree of carination but not morphometrically, since the coefficient of difference is less than 1.28 for every measurable character. If the other Vate shells are considered, the differences between the Vate and Santa Cruz populations practically disappear. Pending further study I have placed the Vate shells in one subspecies, *D. eva eva*, and the Torres, Banks, and Santa Cruz specimens in another, *D. e. stramineus*. Further study is needed on this complex before the classification is settled, however.

Collection of adequate series from the Banks and Torres may necessitate the addition of a name for the Santa Cruz population. Only two adult shells were seen from the Banks (type locality of *stramineus*). Both lacked the color band and were slightly smaller than the Santa Cruz shells. If these differences are constant, the Santa Cruz population could possibly be subspecifically distinct.



**Dendrotrochus (Santotrochus) layardi** (Hartman). Plate 6, figs. 5, 6; plate 7, figs. 3, 4; plate 25, figs. 6-9.

*Oxychona layardi* Hartman, 1889, Proc. Acad. Nat. Sci. Philadelphia, 1889: 91, pl. 5, fig. 2—Aore Island (Delautour).

*Helix (Papuina) layardi* (Hartman), Pilsbry, 1891, Man. Conch., (2), 7: 79-80, pl. 15, figs. 94-97.

*Dendrotrochus layardi* (Hartman), Pilsbry, 1894, Man. Conch., (2), 9: 144; Sykes, 1903, Proc. Malac. Soc. London, 5: 196—Renee River, Espiritu Santo (J. J. Walker); Ancey, 1905, Nautilus, 19, (4), p. 43.

*Trochomorpha (Oxychona) layardi* (Hartman), Mabille, 1895, Bull. Soc. d'hist. Nat. d'Autun, 8: 409—Espiritu Santo (Français).

*Range*.—Aore and Espiritu Santo.

*Material*.—ML 17, ML 31e, ML 32, ML 33, ML 36, ML 74, ML 76, ML 84, ML 95; Aore Island (ANSP 60063 ex Hartman, Layard, Delautour, holotype; ANSP 194310 ex Hartman, Layard, Delautour, paratypes; UMMZ 76501 ex Walker, Ponsonby, Fulton, Layard, type lot; MCZ 182264 ex Fiske-Warren; CM 62.9811 ex Clapp, Hartman, paratype; CM 62.2910 ex Hartman, Layard, paratypes); Hog Harbour, Espiritu Santo (MCZ 147386 M. J. McMillan); Espiritu Santo (UMMZ 162118 ex Walker, Ponsonby); New Hebrides (ANSP 109278 ex Sowerby and Fulton; UMMZ 76502 ex Walker; MCZ 102077 ex Bequaert).

*Remarks*.—The holotype (pl. 25, fig. 8) of *D. layardi* is quite slender, but numerous intergrades connect it with the more obese specimens. Three color variations are found: ashy white (pl. 25, fig. 6); with a dark brown line on the keel and suture (pl. 25, fig. 8); and with an additional brown band between the keel and sutures (pl. 25, fig. 7). All three variations are found in most lots and probably are of no taxonomic significance. Fresh material of *D. layardi* often shows small translucent spots and fine black lines on white background. From the esthetic viewpoint, *D. layardi* is undoubtedly the most "beautiful" snail found in the New Hebrides.

The genital anatomy of *D. layardi* (pl. 7, figs. 3, 4) is typical of *Dendrotrochus*, except for the remarkable internal structure of the penial complex. The "biscuit" at the side of the atrium (pl. 7, fig. 4) is probably stimulatory. It is, however, much too large to fit through the undistended gonopore and the mechanism by which it is everted is unknown. The material available was not suitable for histological study. It could not be ascertained, therefore, whether the "biscuit" contained spaces that, when filled with fluid, resulted in great turgor, or whether it is a solid organ evertable only because of great distention of the gonopore.

The brilliant coloration, trochoidal shell, and radula (pl. 6, fig. 5) suggest that *D. layardi* is an arboreal species. The ecological information with the Kuntz specimens confirms this, since most living specimens were collected on leaves or trunks of trees between 5 and 15 feet from the ground. The radula of *D. layardi* (pl. 6, fig. 5) has developed lateral teeth with all the characteristics of arboreal radulae, that is, with broad, gouge-like cusps (Pilsbry, 1894, p. xiv), while the marginals have the slender, pointed teeth that are characteristic of terrestrial genera. Two radulae of *D. layardi* were mounted. The larger had 118 rows with the formula 151-13-1-13-151; the smaller had 100 rows with the formula 134-12-1-12-134. One dissected specimen had a spermatophore (pl. 6, fig. 6) in the spermatheca. Apparently it is essentially the same as the spermatophores of *D. ponapensis* H. B. Baker (1941, pl. 46, fig. 6). Unlike many zonitids, for example, *Ryssota* (op. cit., pl. 46, fig. 12), the spermatophore of *D. layardi* is without any prominent external sculpture.

### Family ZONITIDAE

Primitively with undivided sole, becoming tripartite when shell is reduced; caudal foss not overhung and often obsolescent or lacking (rarely accentuated when shell is reduced); principal radular marginals not more than bicuspid and more usually unicuspid; amatorial organs or dart-apparatus (when rarely developed) penial; shell usually umbilicate or with open perforation or rimation (H. B. Baker, 1941, p. 205).

The subfamilial relationships within the Zonitidae have been ably discussed by H. B. Baker (1941, p. 270) and Pilsbry (1946b, p. 233). Of the six "restricted" subfamilies recognized by Baker (loc. cit.) only the Trochomorphinae are widely distributed in the Pacific. The Hawaiian Islands have a few endemic species of Zonitinae and Gastrodontinae; otherwise, only introduced species are found on Pacific islands. The Trochomorphinae are an important constituent of the island fauna over most of the Pacific. They probably represent the most advanced land snail taxon native to Polynesia, although they are the most primitive subfamily of the Zonitidae.

### Subfamily TROCHOMORPHINAE

*Trochomorpha*-like shells have been reported from India, Andaman and Nicobar Islands, southeast Asia, China, Japan, the Ryukyus, Formosa, the Philippines, Indonesia, Melanesia (except New Caledonia), Polynesia east to the Society Islands, and the Palau, Caroline, and Marshall islands of Micronesia (fig. 19). None are

known from the Hawaiian, Cook, Austral, Marquesan, or Tuamotu Islands, New Caledonia, Australia, or New Zealand.

The Polynesian and Micronesian Trochomorphae were monographed by H. B. Baker (1941, pp. 270-321). He recognized five genera, *Kondoa*, *Hogolua*, *Brazieria*, *Videna*, and *Trochomorpha*. The first three are restricted to the Caroline Islands; *Videna* ranges from the Palau and Philippine Islands westward(?); and *Trochomorpha* includes the species from Polynesia and Melanesia. It remains for future studies to append the Asian, Indonesian, and Papuan species to Baker's classification. *Videna* and *Trochomorpha* apparently will receive many of the species, but new generic units may be necessary for the Asian shells. Genera extralimital to Baker's study which he included in the Trochomorphae are *Bertia*, *Coxia*, and *Calostropha*, all of Ancey, 1887. The name *Rosselidena* Iredale, 1941, is a nomenclatural unit only, whose status cannot be decided without anatomical investigation.

Several species of *Trochomorpha* (sens. lat.) have been reported from the New Hebridean region. All belong to *Trochomorpha*, except *pulcherrima* Hartman, which seems to be a mislabeled specimen of the Philippine Island *Inozonites bicarinata* (Semper).

#### Genus TROCHOMORPHA Albers, 1850

H. B. Baker (1941, pp. 285-286) divided the Polynesian and Micronesian species of *Trochomorpha* into two subgenera, *Nigritella* for those species without a high, ovoid, penial stimulator and *Trochomorpha* for those species with a stimulator. *Nigritella* is found in the Caroline Islands, Samoa, Fiji, and westward to the Moluccas. *Trochomorpha* (sens. str.) was previously known only from the Tonga and Society Islands. The only Melanesian species examined by Baker was *Trochomorpha sanctae-annae* Smith. On the basis of its unicuspid marginal teeth, Baker established *Lentitrochus* as a new subgenus of *Trochomorpha*. Transitional forms between the radulae of the subgenera *Lentitrochus* and *Nigritella* exist (Solem, in press-A). Pending detailed study of the Solomon Island species I have retained *Lentitrochus* as a subgenus, although it may prove to be a section of *Nigritella*.

The only New Hebridean species of which anatomical material was available, *T. rubens* Hartman, has a well-developed stimulator and thus belongs in *Trochomorpha* (sens. str.). The other New Hebridean species, *T. bakeri*, new sp., is herein tentatively placed in the same section.

Subgenus **TROCHOMORPHA** Albers, 1850

The shell (pl. 24, figs. 1-17) and genital anatomy (pl. 6, figs. 1, 2) of *T. rubens* show several differences from those of the previously described sections of the subgenus *Trochomorpha*. In *T. rubens* the penial stimulator has a short free tip, like the Tongan *Cotitrochus*, but the epiphallus is less sharply differentiated from the vas deferens and the spiral striae of the protoconch present in *Cotitrochus* are absent in *rubens*. The section *Trochomorpha* (sens. str.) differs from *T. rubens* in having a longer free tip of the stimulator, different apical sculpture and more poorly differentiated vas deferens and epiphallus. Probably the penial stimulator in *T. rubens* is not strictly homologous, since it is located near the middle of the penis (see pl. 6, fig. 1). In *Trochomorpha* (sens. str.) and *Cotitrochus* its basal tip lies at or near the junction of the penis and atrium. Because of these differences, a new section is herein established for the New Hebridean species.

**HARTMANITROCHUS**, new section

Penis with several well-developed pilasters and a medial, fusiform stimulator. Vas deferens and epiphallus with longitudinal pilasters; epiphallus entering penis apically but not sharply demarcated from it. No penial sphincter. Shell lenticular to trochiform, apical whorls with weak growth striae and very faint wrinkles similar to those found in *Trochomorpha* (sens. str.).

*Type species.*—*Trochomorpha rubens* Hartman.

*Remarks.*—Retention of *Hartmanitrochus* in the subgenus *Trochomorpha* is for reasons of practicality rather than phylogeny. Apparently development of a penial stimulator has occurred several times in the Trochomorphinae and is an advanced character. The subgenus *Trochomorpha*, with sections in Tonga, Society Islands, and the New Hebrides, is probably composed of parallel termini of separate phylogenetic lines. Until the Indonesian Trochomorphinae have been thoroughly studied, the present classification can be utilized.

Two species, *Trochomorpha rubens* Hartman and *T. bakeri*, new sp., are recognized from the New Hebrides. Quoy and Gaimard (1832-35, p. 127, pl. 10, figs. 22-25) figured a *Trochomorpha* from Vanikoro Island as "*Helix*" *exclusa* Ferussac, a Moluccan species. Photographs (pl. 12, figs. 3-5) of the Vanikoro shell (courtesy of André Franc, Paris Museum) indicate that the figures in Quoy and Gaimard are very inaccurate in portraying the shape of the shell. The photographs show a shell very similar to *T. bakeri* from Aneiteum, but with a narrower, more medial color band and a more convex base. Probably the Vanikoro population represents an undescribed species, but

without personal examination of the original specimen or study of topotypic material, nomenclatural recognition would be unwarranted. In *T. bakeri* the color band is well removed from the carinal sulcus, while in *T. rubens* it borders the carinal sulcus.

**Trochomorpha (Hartmanitrochus) rubens** Hartman. Plate 6, figs. 1, 2, 4; plate 24, figs. 1–11, 14.

*Trochomorpha rubens* Hartman, 1888, Proc. Acad. Nat. Sci. Philadelphia, 1888: 251, pl. 13, figs. 5, 5a, 5b—Aore Island; Pilsbry, 1892, Man. Conch., (2), 8: 129, pl. 57, figs. 1–3; Mabille, 1895, Bull. Soc. d'hist. Nat. d'Autun, 8: 409—Espiritu Santo; Sykes, 1903, Proc. Malac. Soc. London, 5: 196—Terebu and Renee Rivers, Espiritu Santo, Havannah Harbour, Vate (J. J. Walker).

*Trochomorpha convexa* Hartman, 1889, Proc. Acad. Nat. Sci. Philadelphia, 1889: 93, pl. 5, fig. 7—Aore Island; Pilsbry, 1892, Man. Conch., (2), 8: 131–132, pl. 30, figs. 20–25; Mabille, 1895, Bull. Soc. d'hist. Nat. d'Autun, 8: 409—Espiritu Santo (François); Sykes, 1903, Proc. Malac. Soc. London, 5: 196—Terebu and Renee Rivers, Espiritu Santo (J. J. Walker).

?*Trochomorpha* sp. Sykes, 1903, Proc. Malac. Soc. London, 5: 196—Renee River, Espiritu Santo and Ravenga, Vanua Lava (J. J. Walker).

*Range*.—Erromanga, Vate, Malekula, Espiritu Santo and Vanua Lava(?).

*Material*.—ML 9, ML 12 (*convexa*), ML 26 (all vars.), ML 31b (*rubens* to *convexa*), ML 31e, ML 32 (*rubens* and “dome”), ML 33 (all vars.), ML 36, ML 37 (*convexa*), ML 39, ML 44, ML 59, ML 63 (*rubens*), ML 70, ML 74, ML 76, ML 86 (all vars.), ML 95; Aore Island (ANSP 49007, holotype of *rubens*, ex Hartman; ANSP 60062, holotype of *convexa*, ex Hartman; CM 62.4408, paratypes of *convexa*, ex Hartman; CM 62.13887, paratypes of *rubens*, ex Clapp, Hartman; CM 62.4410, paratypes of *rubens*, ex Hartman; CNHM 43675, ex Webb, Gude, Layard, type lot of *rubens*; UMMZ 138890, paratypes of *rubens*, ex Walker, J. H. Thompson; UMMZ 139618, type lot of *rubens*, ex Walker, Ponsonby, Layard; MCZ, topotypes of *convexa*, W. L. Nutting coll. 1944); Segond Channel, Espiritu Santo (ANSP 132673, *convexa*, ex Brazier; CNHM 43629, ex Webb, Gude, Layard; UMMZ 139730, ex Walker, Ponsonby, Layard); Hog Harbour, Espiritu Santo (MCZ, *rubens* to *convexa*, ex J. H. Daniels); Espiritu Santo (UMMZ 161023, *rubens* to *convexa*, ex Walker, Ponsonby; AMNH, *rubens* to “dome,” G. S. Banner, Sept. 9, 1943); Malekula (UMMZ 139617 and 184324, ex Walker, Ponsonby, Melville; Marsh 8604, ex UMMZ, Walker, Ponsonby, Melville); Erromanga (MCZ 12113, ex Layard); New Hebrides (UMMZ 139627, ex Walker, Tomlin).

*Remarks*.—Typologically, *rubens* (pl. 24, fig. 1) differs from *convexa* (pl. 24, fig. 2) in having a flatter spire, a larger diameter, fewer

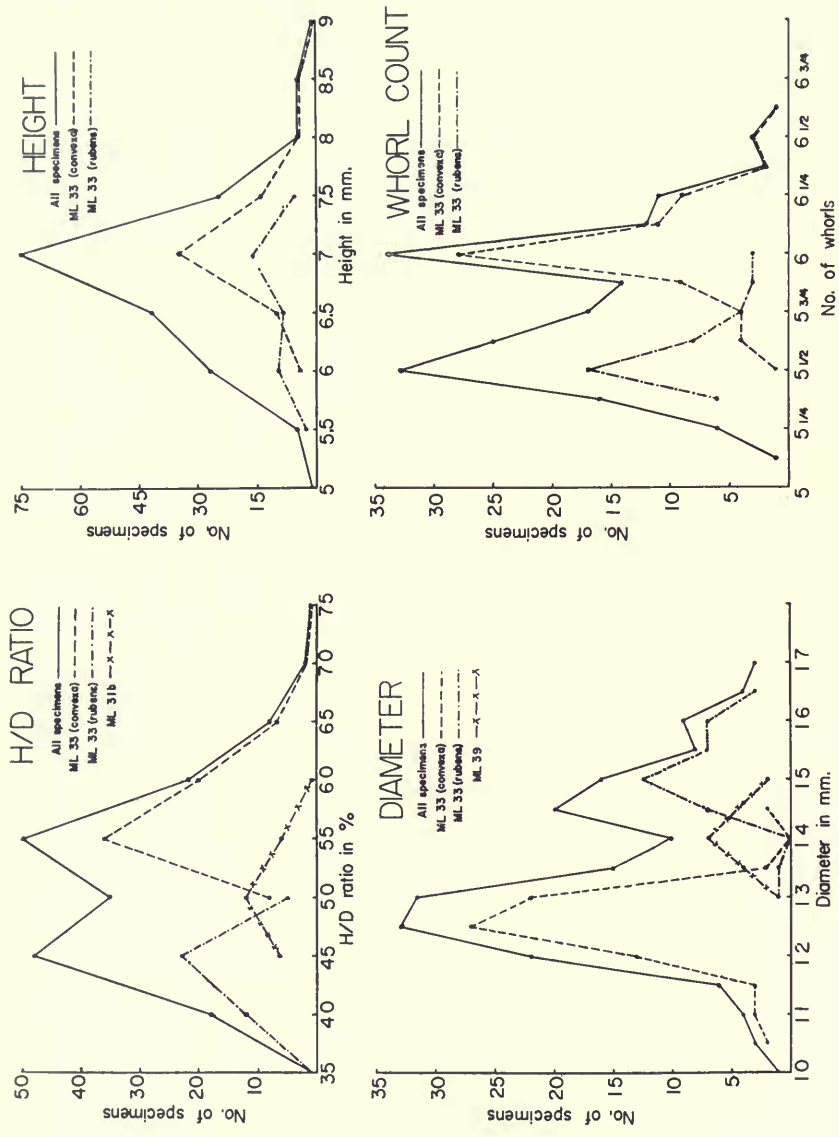


FIG. 4. Variation in *Trochomorpha rubens* Hartman.

Table V.—Size Variation in *Trochomorpha rubens* Hartman

|                  | Total                            | ML 33<br>( <i>rubens</i> ) | ML 33<br>( <i>convexa</i> )      | Live               | Holotype<br>( <i>rubens</i> ) | Holotype<br>( <i>convexa</i> ) |
|------------------|----------------------------------|----------------------------|----------------------------------|--------------------|-------------------------------|--------------------------------|
| No. of specimens | 186                              | 41                         | 74                               | 71                 |                               |                                |
| Height... Mean   | 6.8                              | 6.7                        | 7.2                              | 6.6                | 6.3                           | 6.9                            |
| Range            | 5.0-8.9                          | 5.6-7.5                    | 6.0-8.9                          | 5.0-7.5            |                               |                                |
| S.D.             | 0.63                             | 0.56                       | 0.54                             | 0.57               |                               |                                |
| Diameter... Mean | 13.5                             | 15.4                       | 12.4                             | 13.5               | 14.7                          | 13.1                           |
| Range            | 10.6-17.1                        | 13.2-17.1                  | 10.6-14.5                        | 10.6-16.5          |                               |                                |
| S.D.             | 1.44                             | 0.76                       | 0.62                             | 1.21               |                               |                                |
| H/D... Mean      | 51                               | 44                         | 57                               | 49                 | 42                            | 53                             |
| Range            | 37-74                            | 37-48                      | 49-74                            | 41-64              |                               |                                |
| S.D.             | 7.18                             | 5.24                       | 4.21                             | 5.10               |                               |                                |
| Whorls... Mean   | 5 $\frac{3}{4}$                  | 5 $\frac{5}{8}$            | 6                                | 5 $\frac{3}{4}$    | 5 $\frac{3}{8}$               | 6                              |
| Range            | 5 $\frac{1}{8}$ -6 $\frac{1}{2}$ | 5 $\frac{3}{8}$ -6         | 5 $\frac{1}{2}$ -6 $\frac{1}{2}$ | 5 $\frac{3}{8}$ -6 |                               |                                |

whorls and a more prominent red band. Actually *rubens* is one end of a clinal series, *convexa* is somewhere in the middle, and an unnamed variety, "dome" (pl. 24, figs. 3, 4), is the other extreme. Museum specimens can be fairly easily divided into "*rubens*" and "*convexa*-dome," but the Kuntz material contained numerous intergrades. Including juveniles and museum specimens I saw over 300 individuals of this complex. For statistical analysis, all adult shells collected by Kuntz, that is, those with the lip internally thickened, were measured and the data studied. One lot, ML 33, consisted of a thanatocoenosis of 115 adult shells from a road cut in the Sarakata River Valley. Before this study was started, the lot had been divided into "*rubens*" and "*convexa*-dome." The series were analyzed separately and significant morphometric differences found between them (see Table V and fig. 4). Examination of "live" material (71 adults) showed mainly intermediate specimens, one lot, ML 31b (pl. 24, figs. 5-11, 14), containing a complete series while other lots, ML 26, ML 32, ML 39 and ML 86, had less complete series of intergrades. Intergrades were most common between the nomenclatural types of *rubens* and *convexa* and less frequent between *convexa* and "dome."

Animals of all forms were available, and two of each variety were dissected. No taxonomically significant variations were found in the radula (pl. 6, fig. 4) or the genitalia (pl. 6, figs. 1, 2). The radular formula was (29-33)-(10-13)-1-(10-13)-(28-33)  $\times$  115-130. The teeth are quite typical, with the bicuspid marginals of *Trochomorpha* (sens. str.) and *Nigritella*. The unusual features of the genitalia are

discussed under the sectional description of *Hartmanitrochus*. No major anatomical differences exist between "rubens" and "convexa-dome." There is, however, an indication of slight differences in the proportions of the mantle organs and parts of the genitalia. The differences are small, and not enough material was available to prove whether or not they are statistically significant.

Despite the lack of specific anatomical characters and the intermediate nature of the shells of living specimens, the fact remains that museum specimens and the subfossil material from lot ML 33 can be divided into two series which are significantly different morphologically. According to Mayr, Linsley and Usinger (1953, p. 146), the two series mentioned above are well above the conventional limit of subspecific discrimination in respect to diameter (coefficient of difference 2.18) and H/D ratio (C.D. 1.38). There is no possibility of geographic isolation, since the forms are sympatric (ML 26, ML 31b, etc.). Apparently, however, there is an ecologic difference, as most specimens of "rubens" were collected on the ground and most specimens of "convexa-dome" on trees. A similar case of habitat subspeciation is found in *Trochomorpha nigritella* (Pfeiffer) from Ponape in the Caroline islands (H. B. Baker, 1941, pp. 292-294), and actual ecological speciation occurs in the Raiatean *Trochomorpha typus* H. B. Baker and *T. swainsoni* (Pfeiffer) (H. B. Baker, 1941, p. 318). In the case of the New Hebridean *T. rubens* complex, field studies are needed to establish the exact degree of ecological separation.

All the museum specimens of *T. rubens* were collected prior to the wide-scale establishment of plantations; indeed, most of them were found by new settlers while they were clearing land for planting. The subfossil specimens from ML 33 almost certainly were deposited long before extensive cultivation was practiced. These specimens can be easily divided into *rubens* and *convexa*-"dome" and intergrading individuals are few. The living material collected by Kuntz had a much higher percentage of intergrading individuals and was mainly obtained at or near the boundary between jungle and plantation. There is also a possibility that "rubens" and "convexa-dome" are well differentiated and isolated in natural jungle areas, but that in cultivated or ecotonal areas the complete or partial isolation breaks down.

Without field studies the exact relationship of "rubens" and "convexa-dome" must remain uncertain. On the basis of variation found in the Kuntz material, they are here united in a single species. How-



ever, they may be ecologically isolated subspecies or even species which hybridize under "artificial" plantation conditions.

The distributional limits of the *rubens* complex is uncertain. Specimens from Malekula are conchologically identical with typical *rubens* as is the single specimen seen from Erromanga. No material from Vate was available, nor could I determine the status of the form reported by Sykes from Vanua Lava and Espiritu Santo as "approaching *approximata*." The presence of *rubens* on Malekula is not surprising, but the Erromanga record needs confirmation, particularly since Layard, in a letter to Hartman (March 17, 1888) refers to *bakeri* as living on both Aneiteum and Erromanga.

**Trochomorpha (Hartmanitrochus) bakeri**, new species. Plate 24, figs. 13, 15-17.

*Helix apia* Pfeiffer (not Hombron and Jacquinot, 1852), 1854, Conch. Icon., *Helix*, pl. 199, fig. 1402—Aneiteum (MacGillivray); Pfeiffer, 1859, Mon. Helic. viv., 4: 183—New Hebrides; Tryon, 1887, Man. Conch., (2), 3: 88, pl. 17, figs. 45-46—New Hebrides.

*Helix (Discus) apia* Pfeiffer (not Hombron and Jacquinot, 1852), Cox, 1868, Exchange list, p. 38, no. 7—Aneiteum.

A species of *Trochomorpha* distinguished from the *rubens* complex by its heavier shell, coarser surface sculpture, sharper, wider keel, and lighter ground color, and by having the spiral color band well removed from the carinal sulcus. The anatomy is unknown.

Shell lenticular to trochiform, thick, solid, base slightly convex; carinate, with a broad, prominent sulcus above the periphery, greatly reduced below. Straw-colored, with (or without) supracarinal and basal red spiral bands well removed from the straw-colored carina. Sculpture of equally vague protractive and retractive striae, crossed by prominent growth wrinkles on the later whorls. Embryonic whorls with fainter sculpture than the spire, eroded in most adults. Aperture ovately rostrate, upper lip thin, slightly indented, lower lip strongly thickened internally. Parietal callus thin. Umbilicus variable in size, 1.8-2.3 mm. in diameter, contained 6.3-9 times in the base. Diameter of holotype 14.5 mm., height 7.8 mm., whorls  $5\frac{1}{2}$ ; umbilicus 2.2 mm., contained 6.5 times in the diameter.

*Type*.—University of Michigan Museum of Zoology no. 184722. Collected on Aneiteum Island, New Hebrides. Specimen from the Walker collection.

*Paratypes*.—The following specimens examined during this study may be considered paratypes: Aneiteum (UMMZ 139690, ex Walker, Ponsonby, Layard, the "type lot"; AMNH, Macmillan!, 1937; CM 62.4406, ex Hartman, Layard; CM 62.13885, ex Clapp, Mazyck, Layard; CNHM 43696, ex Webb, Gude, Layard); New Hebrides (MCZ, ex Thaenum, Shackelford; MCZ, from unknown source;

UMMZ 139689, ex Walker, Tomlin; UMMZ 139691, ex Walker, Ponsonby; ANSP 1932, ex A. D. Brown; Marsh 8544, ex UMMZ, Walker, Ponsonby).

*Range*.—Aneiteum, but may be found on Tanna and Erromanga.

*Remarks*.—H. B. Baker (1941, pp. 311–313) restricted the name *apia* Hombron and Jacquinot, 1852, to a Samoan shell and pointed out the error in using *apia* for the New Hebridean species. Since the New Hebridean species were not included in Baker's monograph, he did not propose a new name, based on Reeve's illustration, for the Aneiteum species. Great pleasure is taken in naming this species after Dr. Baker in appreciation of his invaluable assistance.

*T. bakeri* is superficially similar to the Samoan *T. apia*, but the latter has on the embryonic whorls a strong spiral sculpture which is lacking in *T. bakeri*. Although the anatomy of *T. bakeri* is unknown, there can be little doubt that it is closely related to the *rubens* complex. The sculpture of the two species is identical and the variations in contour and size are quite similar. *T. bakeri* has been given specific status on the basis of the differences noted in the diagnosis. With the exception of the position of the color band (pl. 24, fig. 13) all of the differences can be considered as adaptations to the drier climate of Aneiteum; increase in shell thickness, prominence of growth wrinkles and lightening of coloration are all well-documented adaptations of snails to xeric conditions. The position of the color band has proven to be indicative of specific differences in other island groups, so that, despite lack of anatomical material, specific status for *T. bakeri* is warranted. A series of specimens showing variation in contour and color is illustrated (pl. 24). The morphometry of the twenty-seven available specimens is summarized in Table VI.

Table VI.—Size Variation in *Trochomorpha bakeri*

|            | Height  | Diameter  | H/D   | Whorls                           |
|------------|---------|-----------|-------|----------------------------------|
| Mean.....  | 7.4     | 15.1      | 49    | 5 $\frac{3}{8}$                  |
| Range..... | 6.5–9.2 | 13.6–16.3 | 42–62 | 5 $\frac{1}{8}$ –5 $\frac{7}{8}$ |
| S.D.....   | 0.55    | 0.73      | 5.07  |                                  |

Through the courtesy of Dr. Donald F. McMichael of the Australian Museum (Sydney), it was possible to determine the identity of most of the unfigured species described by Cox (1870). One "zonitid," *Helix vannaelavae* Cox, 1870, could not be located in the Australian Museum collection and its identity remains unknown. The original description is reprinted below.

***Helix vannaelavae* Cox.**

*Helix vannaelavae* Cox, 1870, Proc. Zool. Soc. London, 1870: 82-83—Aneiteum (Brazier!).

Shell imperforate, conoidly depressed, dark yellowish horn colour, smooth, shining; spire broadly conoid; whorls  $5\frac{1}{2}$ , only slightly convex, last not descending, base convex; suture shallow; aperture lunate; peristome thin, simple, columellar margin a little dilated above. Diam., greatest 0.14, least 0.12; height 0.11 of an inch.

No shell seen during this study even slightly approximated the brief description. The four small zonitoid snails known from Aneiteum, *Coneuplecta (Sitalina) microconus*, *Liardetia samoensis*, *Lamprocystis guttula*, and *Orpiella retardata*, all have conspicuous umbilici and a different shape than *Helix vannaelavae*.

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Specimens of the following two species were in museum collections with a label stating they were from the New Hebrides. They almost certainly represent mislabeled specimens rather than valid records.

***Inozonites bicarinata* (Semper). Plate 24, fig. 12.**

*Euplecta bicarinata* Semper, 1870, Reisen im Philippinem, (2), 3: 16-17, pl. 2, fig. 8a-c—Bery Arayat, Pampanga, Luzon, Philippine Islands; Faustino, 1930, Philippine Jour. Sci., 42, (1), p. 95—Luzon.

*Trochomorpha pulcherrima* Hartman, 1890, Proc. Acad. Nat. Sci. Philadelphia, 1890: 288, pl. 3, fig. 13—Aore Island, New Hebrides.

*Range*.—Luzon, Philippine Islands.

*Material*.—Aore, New Hebrides (CM 62.5825, ex Hartman, Layard, holotype of *pulcherrima* Hartman); Morong, Luzon (UMMZ 79824, ex Walker, Ponsonby, Moellendorff; ANSP 63988, ex Moellendorff); Manila, Luzon (ANSP 148327, ex Walker, Fulton).

*Remarks*.—The unique holotype of *pulcherrima* cannot be distinguished from Philippine specimens of *Inozonites bicarinata*. Probably either Layard or Hartman mixed the Philippine shell with New Hebridean material in packing specimens for shipment. The holotype of *pulcherrima* measures 6.2 mm. in height and 11.8 mm. in diameter, and has six whorls.

***Mendaña (Tahuatoa) garrettiana* (Garrett)**

A single specimen of this Marquesan species was in a lot of *Orpiella retardata retardata* (Cox) from Vate Island (UMMZ 147918, ex

Walker, Ponsonby, Ancey, Layard). Ancey had material of *M. garrettiana* (see H. B. Baker, 1938b, pp. 37-38, pl. 15, figs. 3, 4) at the same time (1883-89) that he was receiving New Hebridean shells. It is quite possible that specimens became mixed in preparing exchange collections.

### Suborder HOLOPODA Pilsbry, 1896

Sigmurethrous snails with the pedal grooves usually rather inconspicuous and at or close to the angle of the foot. (After Pilsbry, 1946b, p. 231.)

Several groups of families can be recognized within the Holopoda, but because relationships are still uncertain, no taxa above the family have been formally recognized below. The content and distribution of the broad categories are briefly summarized, and discussions of their characteristics can easily be found in Pilsbry (1894, 1900a) and Thiele (1931) or the cited references.

Watson (1915) demonstrated the polyphyletic nature of Pelseener's Agnatha, but there are still several families which seem to be more closely related to each other than to any of the herbivorous taxa. Further study may reveal their vegetarian ancestors, but until then the Agnathomorpha remains a useful concept. Pilsbry (1900a, 1908), Watson (1915), and H. B. Baker (1930, p. 408) pointed out that the Aperidae, Haplotrematidae, Streptaxidae, and Paryphantidae possess many characteristics in common and may be phylogenetically related. Watson (1915) derived both the Aperidae and Streptaxidae from primitive paryphantids. The relationship of the Haplotrematidae is less certain, but it has been included here on the authority of H. B. Baker.

The great majority of the holopod snails have a vegetarian diet. Our knowledge of their classification is still essentially that of Pilsbry (1894, 1900a) as subsequently modified by Pilsbry himself.

The herbivorous holopod Sigmurethra consist of five groups: the Achatinacea, Bulimulacea, Polygyracea, Helicacea, and Clausiliacea. Only the Bulimulacea are native to the New Hebrides,<sup>1</sup> but a brief survey of the distribution of the others is included for subsequent reference.

The Achatinacea are predominately African, but several genera seem to be native to the West Indian-Brazilian region (Pilsbry, 1906, p. vi), and the relict family Megaspiridae is found in Brazil, Obi in

<sup>1</sup>The genus *Draparnaudia* (p. 121) has been left in the helicacean family Camaenidae, but its position is doubtful.

the Moluccas, New Guinea, and Queensland. A few small achatinaceans have been widely spread by commerce and are now practically ubiquitous.

The Bulimulacea are primarily South and Middle American, with two taxa, *Bothriembryon* and *Placostylus*, in the Pacific and possibly one genus, *Prestonella* (see p. 123), in South Africa. The Bulimulidae are found throughout Middle and South America with *Bothriembryon* and *Placostylus* in the Pacific and *Prestonella* in Africa. Iredale (1937a, 1944) created families for the two Pacific taxa, but I am ignoring his action. The other family, the Urocoptidae, is found in the West Indies, Central America, and northern South America, and a few species reach the southwestern United States.

The Clausiliacea are found in Europe, northern Africa, Asia, South America, and the West Indies. A few species (fig. 14) reach the Indo-Australian archipelago (see Loosjes, 1953), and one species has been found in New Guinea (Loosjes, 1956). The Clausiliacea are of uncertain affinities, but H. B. Baker (1956a, p. 131) suggests that they may be related to the Bulimulacea.

The Polygyracea (Pilsbry, 1948, p. vi) probably are the most primitive existing stock of the true helices. They are restricted to North and Middle America and are the only holopod mollusks found in eastern North America. The western part of North America served as a causeway for the helices which populated the West Indies, Central and South America, but none were able to cross the Great Plains region.

The Helicacea represent the most advanced land snails. Within this broad taxon, many families can be recognized. The more primitive families are found in southern areas; the more specialized families are northern in distribution. The over-all pattern of distribution has been interpreted to indicate a southern Asian origin for the Helicacea.

Of all the holopod superfamilies, only the Agnathomorpha and Bulimulacea are native to the New Hebrides. The Helicacea may possibly be represented by *Draparnaudia* but until its anatomy has been fully studied, it is uncertain whether *Draparnaudia* is a bulimulid, a camaenid, or an orthurethrous tornatellinid.

No attempt has been made to define the higher taxa of the several introduced holopods, or to characterize the superfamilial categories outlined above.

## Family SUBULINIDAE

Many subulinids have been accidentally imported on plants into tropical countries or greenhouses of the temperate zone. Thaanum (1927) illustrated the frequency with which they are found during customs inspection of plants and produce entering Hawaii. The subulinids found in the New Hebrides are obvious importations; for a full discussion of their classification see Pilsbry (1946b).

*Subulina octona* is the largest of the three species. It is imperforate at all stages of growth and has much larger nuclear whorls than *Lamellaxis gracilis*, which is perforate in young shells and has rather small nuclear whorls. *Opeas pumilum* is characterized by its sinuous lip and arcuate sculpture. Sykes (1903, p. 198) reported *Lamellaxis oparanum* (Pfeiffer) from Vate, Vanua Lava, and Valua. Probably the record was based on the ubiquitous *L. gracilis*. Other wide-ranging subulinids such as *Lamellaxis micra* (Orbigny) and *L. mauritianum* (Pfeiffer) will eventually be found in the New Hebrides.

**Subulina octona** (Bruguere)

*Bulimus octonus* Bruguere, 1792, *Encycl. Meth.*, I, p. 325.

*Subulina octona* (Chemnitz), Sykes, 1903, *Proc. Malac. Soc. London*, 5: 198—Vila, Vate, New Hebrides.

*Subulina octona* (Bruguere), Pilsbry, 1906, *Man. Conch.*, (2), 18: 72, pl. 12, figs. 8, 9; van Benthem Jutting, 1952, *Treubia*, 21, (2), pp. 376–378, figs. 52–53.

*Range*.—Vate, Epi, and Espiritu Santo. Circumtropical.

*Material*.—ML 8, ML 14, ML 21, ML 23, ML 26, ML 31, ML 34, ML 39, ML 49, ML 69, ML 70, ML 95; Vila, Vate (USNM 598357, Miller!); Vate (DMNZ, W. H. Dawbin!); Nivenue, Epi (DMNZ, A. G. Horwell!).

*Remarks*.—*Subulina octona* probably was native to the Western Hemisphere and introduced into the Pacific in comparatively recent times (Pilsbry, 1906, p. 74). In the New Hebrides it is very common in cultivated areas and near houses. Although it is found under decaying logs, sticks, and leaves, its favorite habitat seems to be in decaying coconuts.

**Opeas pumilum** (Pfeiffer)

*Helix goodalli* Miller, 1822, *Ann. Phil.*, n.s., 3: 381 (not Ferussac, 1821).

*Bulimus pumilus* Pfeiffer, 1840, *Arch. Naturg.*, p. 252.

*Opeas pumilum* (Pfeiffer), Pilsbry, 1946, *Monog. N. Amer. Land Shells*, 2, (1), pp. 181–182.

*Range*.—Espiritu Santo and Vate. Circumtropical.

*Material*.—ML 95; Vate (DMNZ, W. H. Dawbin!).

*Remarks*.—The small nuclear whorls and obese shape separate *O. pumilum* from *Subulina octona*. *Lamellaxis gracilis* is much slenderer and has stronger sculpture than the other two species.

### **Lamellaxis (Allopeas) gracilis (Hutton)**

*Bulimus gracilis* Hutton, 1834, Jour. Asiat. Soc. Bengal, 3: 93.

*Stenogyra juncea* Mabile (not Gould), 1895, Bull. Soc. d'Hist. Nat. d'Autun, 8: 411—New Hebrides.

*Opeas gracile* (Hutton), Pilsbry, 1906, Man. Conch., (2), 18: 125–132, pl. 18, figs. 3–6; van Benthem Jutting, 1952, Treubia, 21, (2), pp. 378–380, figs. 55, 56a.

*Range*.—Aneiteum and Espiritu Santo. Circumtropical.

*Material*.—ML 8, ML 14, ML 23, ML 31c, ML 33, ML 35, ML 39, ML 69, ML 74, ML 76, ML 95; Espiritu Santo (USNM 432453, Harrington!); Aneiteum (AMNH; DMNZ, W. H. Dawbin!).

*Remarks*.—Although *L. gracilis* and *Subulina octona* were found together at four localities on Espiritu Santo (excluding the drift sample, ML 95), most of the specimens were collected at different sites. Possibly the two species are partially ecologically isolated, but no definite data are available.

### Family BRADYBAENIDAE (=Eulotidae)

Key references to the classification of the Bradybaenidae are Connolly (1939) and Pilsbry (1939, p. 15). The only species found in the New Hebrides, *Bradybaena similaris* (Ferussac), has been widely distributed by commerce.

### **Bradybaena similaris (Ferussac)**

*Helix similaris* Ferussac, 1821, Tabl. Syst. Limacons, 3: 47.

*Bradybaena similaris* Ferussac, van Benthem Jutting, 1950, Treubia, 20, (3), pp. 501–503, figs. 104–105.

*Range*.—Vate and Espiritu Santo. Circumtropical.

*Material*.—ML 18, ML 20, ML 26, ML 31c, ML 31e, ML 34, ML 39, ML 44, ML 50, ML 51, ML 63, ML 64, ML 66, ML 70, ML 94; Vila, Vate (Miller, USNM 598356).

*Remarks*.—*Bradybaena similaris* is native in eastern Asia from southern China to Java and Celebes. There it lives in the “wild” as well as in “cultivated” areas. Opinions differ as to the means of

dispersal. Many consider that it has traveled with the coffee tree, but Pilsbry (1894, pp. 203–204) suggested that sugar cane serves as a more likely carrier.

Both banded and unbanded shells were found, occasionally in equal numbers, sometimes with one predominating. Van Benthem Jutting (loc. cit.) gave a good summary of the distribution, variation, and ecology of this species, and Komai and Emura (1955) analyzed the genetical basis for its color variation.

### Family CAMAENIDAE (=Pleurodontidae)

Helices without dart apparatus; penis continued in an epiphallus and a flagellum (the latter sometimes vestigial or wanting); spermathecal duct not branched (Pilsbry, 1939, p. 411).

Camaenids are widely distributed in the Indo-Australian and American tropics, and in the Palaeo-Oriental land snail region they form the "dominant" land snail taxon. Both anatomy and distribution place the camaenids as more primitive than and ancestral to the dart-bearing helicids of Eurasia and western North America (see Pilsbry, 1894). The camaenids have occupied a number of habitats, producing such terrestrial genera as *Chloritis* (sens. lat.), *Thersites*, and *Rhagada*, arboreal genera such as *Papuina* and *Amphidromus*, and desert snails such as *Glyptorhagada* and *Xanthomelon*.

Iredale (1937b, 1938, 1941) grouped the Austro-Melanesian species into several "families." Few Austro-Melanesian species have been dissected, but the published data show the same types and extent of variations that are found in the West Indian camaenids (see Wurtz, 1955). Iredale's creation of families for *Chloritis*, *Papuina*, *Xanthomelon*, *Hadra*, and *Rhagada* ignores important and obvious affinities to such Malayan taxa as *Amphidromus*, *Landouria*, and *Ganesella*. The West Indian genera show an equal amount of conchological variation, and careful study of their anatomy has shown their essentially similar basic structure.

Iredale is consistently unable to recognize that diversity in conchology is often produced by ecological adaptations and that arboreal and terrestrial genera such as *Papuina* and *Chloritis*, despite strikingly different shells, are actually closely related.

Many "*Papuina*" and "*Chloritis*" are found in the Solomons, Bismarcks, and New Guinea, but none have been found on any New Hebridean island. Jaeckel and Schlesch (1952, pp. 157–158, pl. 6, figs. 5a–c; see also Watson, 1953, pp. 99–100) described *Papuina*



*charlottae* from a single shell supposedly found on Santa Cruz Island. *P. charlottae* is closely related to the Guadalcanal *P. caeruleascens* Angas and an unnamed form from Florida Island, Solomon Islands (Solem, in press-A). Iredale (1927) did not mention any Santa Cruz *Papuina*, nor were any collected by W. M. Mann. It is suspected that *Papuina charlottae* was actually collected in the Solomons rather than on Santa Cruz Island because there are other errors in Jaeckel and Schlesch (1952), only a single specimen is known, and the source of the specimen has been responsible for other locality errors. The presence of a *Papuina* on Santa Cruz Island would be very significant zoogeographically, but the record of Jaeckel and Schlesch cannot be accepted as valid.

A genus of small terrestrial snails found in the New Hebrides, Loyalties, and New Caledonia (fig. 17), *Draparnaudia*, usually has been placed in the Camaenidae. Its resemblance to a miniature *Amphidromus* or *Pseudopartula* perhaps influenced its inclusion in the Camaenidae rather than the Bulimulidae. The shells which most resemble *Draparnaudia* belong to the Hawaiian tornatellinid genus *Auriculella*.

#### Genus *Draparnaudia* Montrouzier, 1859

Shell small, sinistral, perforate, turbinate-conic, covered with a yellow or brown cuticle. Whorls  $5\frac{1}{2}$  to 7, convex, very obliquely striated. Aperture very oblique, truncate-oval, the peristome expanded or simple, columellar margin broadly dilated and built forward, columella simply reflexed (Pilsbry, 1901, p. 13).

*Type species*.—*Draparnaudia michaudi* Montrouzier (= *Helix sinistrorsa* Deshayes, 1840).

Moss and Webb (1897) figured the jaw, radula, and terminal genitalia of *Draparnaudia lifuana* Pilsbry. Pilsbry (1899), placed *Draparnaudia* in the Camaenidae on the basis of those illustrations but stated that "until the pallial region is investigated, we cannot be certain that it is not a member of the *Bulimulidae*." On the basis of the published drawings of the anatomy, I consider it probable that *Draparnaudia* represents a tornatellinid which has lost the penial appendage rather than a camaenid which has lost the characteristic flagellum. Without study of the pallial region, however, speculation on affinities is useless, and I have left the species, with some hesitation, in the Camaenidae.

Six species and a number of varieties of *Draparnaudia* have been recognized (Pilsbry, 1901, pp. 12-18, 283, lxxi; Sykes, 1903; and

Ancey, 1905). The species from New Caledonia and the Loyalty Islands have been reviewed by Franc (1957, pp. 162-164). The New Hebridean species are reviewed below.

Key to the New Hebridean *Draparnaudia*

1. Shell less than 7 mm. high; six whorls; obtusely or not keeled at the periphery. . . 2  
Shell 9-10 mm. high; 6 $\frac{3}{4}$  whorls; acutely keeled at periphery.  
*D. s. singularis* (Pfeiffer)
2. Shell rounded at periphery of body whorl; Espiritu Santo. . . *D. walkeri* Sykes  
Shell obtusely keeled at periphery; last whorl not deflected in front; Aneiteum.  
*D. s. diminuta* Ancey

***Draparnaudia singularis singularis* (Pfeiffer).** Plate 8, fig. 7.

*Helix singularis* Pfeiffer, 1854, Proc. Zool. Soc. London, 1854: 290—Aneiteum (MacGillivray!).

*Helix (Geotrochus) singularis* Pfeiffer, Cox, 1868, Exchange List, p. 44, no. 103—Aneiteum.

*Bulimus sinistrorsus* var. *carinatus* Gassies, 1876, Faune Conchy. N. Caledonie, 2: 92—Isle of Pines.

*Draparnaudia singularis* (Pfeiffer), Pilsbry, 1901, Man. Conch., (2), 14: 14-15, pl. 3, fig. 1; Dautzenberg, 1923, Nova Caledonia, 3, (1), p. 143—Uvea, Loyalty Islands; Franc, 1957, Mem. Mus. d'Hist. Nat., (n.s.), Zool., 13: 162-163, pl. 21, fig. 216.

*Range*.—Aneiteum. New Caledonia and Loyalty Islands.

*Material*.—New Hebrides (ANSP 31512); New Caledonia (MCZ 74686, UMMZ 145974); Isle of Pines (UMMZ 146973). Photograph of holotype (BM).

*Remarks*.—*Draparnaudia singularis* is the only species of land snail found in both New Caledonia and the New Hebrides which has not been obviously introduced by man. I have based the specific identity of the New Hebridean and New Caledonian specimens on a comparison of the photograph of the holotype with New Caledonian shells, since no New Hebridean material with exact locality data was available to me. The very prominent thread-like keel on the body whorl easily separates *D. s. singularis* from the other New Hebridean morphs.

***Draparnaudia singularis diminuta* Ancey**

*Draparnaudia singularis* Ancey (not Pfeiffer), 1897, Nautilus, 11: 27—Aneiteum.

*Draparnaudia singularis diminuta* Ancey, 1905, Nautilus, 19: 42-43—Aneiteum.

*Range*.—Aneiteum.

*Material*.—No material available.

*Remarks.*—According to the original description, this variety is smaller and less acutely keeled than typical *singularis*. It has not been figured, and I have examined no specimens.

**Draparnaudia walkeri** Sykes. Plate 8, fig. 8.

*Draparnaudia walkeri* Sykes, 1903, Proc. Malac. Soc. London, 5: 197, fig. 2—  
Renee River, Espiritu Santo.

*Range.*—Espiritu Santo.

*Material.*—ML 95. Photograph of holotype (BM).

*Remarks.*—The small size and slightly keeled periphery distinguish *D. walkeri* from *D. s. singularis*. According to Ancey (1905, pp. 42–43), *D. walkeri* has a higher body whorl and more rounded periphery than *D. s. diminuta*. A juvenile specimen collected by Kuntz has been referred here, although it is too young to have developed the characters used in specific determination.

### Family BULIMULIDAE

Shell ovate to cylindrical. Body without visible pedal grooves. Kidney short, triangular, cardiac edge equal to pericardium in length, secondary ureter complete. Penis entering epiphallus without external distinction; epiphallus often continued in a flagelliform appendage. Penial retractor attached at or near end of flagellum or epiphallus. Jaw composed of vertical or medially converging imbricating plates. Radula of helicid type; central tooth as wide as adjacent laterals or somewhat narrower. Right ocular retractor muscle arising from columellar muscle; left ocular united shortly or for some distance with pharyngeal retractor. (Adapted from Pilsbry, 1946b, p. 1.)

The Bulimulidae are primarily South American, reaching maximum development in Brazil, where seventeen genera are found (Pilsbry, 1946b, p. 2). A few genera extend north into Mexico, the West Indies, and the southern United States; others are found in Australia, New Zealand, and Melanesia (fig. 15). Two African genera, *Aillya* (see pp. 33, 35) and *Prestonella* (see Connolly, 1939), have been referred to the Bulimulidae, but their taxonomic position is uncertain. H. B. Baker (1955) considers *Aillya* to be a relative of the Succineidae, and (personal communication) thinks that *Prestonella* may also belong to the Heterurethra. No study on the anatomy of *Prestonella* has been published, and determination of its affinities must await dissection of the animal.

The exact phylogeny of the Bulimulidae is uncertain, but the present distribution, comparative anatomy and fossil record suggest a South American adaptive radiation in the Mesozoic and Tertiary.

Fossil bulimulids, in many cases referable to modern genera, are found in the Eocene and Paleocene of Patagonia. In Brazil, bulimulids do not appear until the middle Tertiary (Parodiz, 1946, 1949). Outside of South America, the only known fossil bulimulids are from the Miocene of Florida. The genus occurring there, *Hyperaulax*, still lives on Fernando Noronha off Brazil and is a primitive member of the Odontostominae. During the Miocene, Florida land snails were Antillean in affinities and origin. The living *Hyperaulax* may be the last remnant of an early northward radiation which reached the insular fringes in the Miocene but has later been replaced by more advanced bulimulids.

Apparently the bulimulids are entering North America in the wake of the warming climate.

The affinities of the Austro-Melanesian bulimulids have long been doubtful. Iredale (1937a, 1944) created separate families for the two Austro-Melanesian taxa, *Bothriembryon* and *Placostylus*. Recent studies by Pilsbry (1946a) and Kondo (1948) reaffirmed the bulimulid relationship of both genera. Their positions within the family differ, however.

*Bothriembryon* (fig. 20) is found in southwest Australia and Tasmania. The northern limit seems to be Shark's Bay, the eastern limit is Port Lincoln, and there is a single species in Tasmania. Iredale (1933, 1937a, 1939) studied *Bothriembryon* and in the process proposed at least eight new generic or subgeneric names and twenty-three new specific ones.

The embryonic shell sculpture varies widely, and exactly parallels the variations found in South American *Bulimulus* (Pilsbry, 1900c, pp. 1-2, pl. 4). The central Australian *Bothriembryon spenceri* Tate and the Tasmanian *B. gunnii* (Sowerby) (= *tasmanicus* Pfeiffer) have the most primitive embryonic sculpture, and the species of King George's Sound have the most advanced type. Probably this indicates a secondary radiation from a southwest Australian "refuge zone" rather than an original radiation from south to north. The area in which *Bothriembryon* lives has a very limited molluscan fauna and only recently has been re-united to the rest of Australia. Previously the large central sea and desert provided effective isolating mechanisms.

Pilsbry (1901, p. 1; 1946a) examined the anatomy of *Bothriembryon* and found it essentially the same as the more primitive South American bulimulids. On the basis of conchology, ecology, and anat-

omy there is absolutely no basis for more than generic separation of *Bothriembryon* and *Bulimulus*.

Both Pilsbry (1901) and Kondo (1948) dissected *Placostylus*. In most characters it is the same as the South American bulimuline genera, but the shortened spermathecal duct, very capacious penis, and rather enlarged pericardial vein of the species studied led Pilsbry (1946a) to propose a subfamily, the Placostylinae, for *Placostylus* and *Diplomorpha*. Iredale (1944, p. 309) listed a name, Placostylinae, but gave no diagnosis or identifying characters. The International Rules of Zoological Nomenclature, at the present time (Hemming, 1953, p. 35, paragraph 52), accept such nomina nuda as being nomenclaturally published. If priority for family names is accepted, Iredale must be credited with the family name, although Pilsbry is certainly the taxonomic author.

Actually the anatomy of *Diplomorpha* (see Kondo, 1948) and the New Hebridean *Placostylus* (see p. 128) is transitional between the generalized South American Bulimulinae and *Bothriembryon* and the specialized *Placostylus* on which Pilsbry based his Placostylinae. The subfamily Placostylinae is weakly differentiated, but it can be retained in the classification pending more comprehensive investigations.

If *Dryptus* is added and *Prestonella*, *Aillya*, *Partula*, and *Peltella* are removed, the classification of the Bulimulidae in Thiele (1931) adequately summarizes the New World Bulimulidae. The Placostylinae are considered in detail below.

### Subfamily PLACOSTYLINAE

Bulimulidae with a short, capacious penis, enlarged first branch of the pericardial vein, and shortened spermatheca (in some species). (Modified from Pilsbry, 1946a, p. 3.)

In this study only two genera are recognized in the Placostylinae. *Placostylus* will probably be split into genera along the lines indicated below, but further study is needed before additional units should be recognized. *Diplomorpha* is restricted to the New Hebrides.

#### Key to the New Hebridean Placostylinae

1. Shell large, height more than 29 mm.....*Placostylus* 2  
Shell small, height less than 29 mm.....*Diplomorpha* 4
2. Umbilical chink completely closed.....*fuliginus* (Pfeiffer)  
Umbilical chink partially to widely open.....3

3. Shell thin, without prominent surface sculpture; habitat arboreal.
- (a) Espiritu Santo . . . . . *bicolor* (Hartman)
- (b) Erromanga . . . . . *turneri* (Pfeiffer)
- Shell thick, with prominent surface sculpture; habitat terrestrial.
- (a) Santa Cruz Island; apical sculpture with 10 ridges/mm.
- hullianus* (Iredale)
- (b) Aneiteum to Espiritu Santo; apical sculpture with 18 ridges/mm.
- salomonis* (Pfeiffer)
4. Shell ovate,  $3\frac{1}{2}$ - $4\frac{3}{4}$  whorls . . . . . *Diplomorpha* (sens. str.) 5
- Shell elongate,  $4\frac{7}{8}$ - $5\frac{3}{8}$  whorls, surface with longitudinal sculpture.
- Diplomorpha* (*Quiros*) *bernieri* (Hartman)
5. Shell with a distinct parietal tooth . . . . . *layardi* Ancey
- Shell without a parietal tooth . . . . . 6
6. From southern New Hebrides (Aneiteum?) . . . . . *coxi* (Pease)
- From Espiritu Santo or outlying islands . . . . . 7
7. Reflexed portion of lip orange, lip only slightly expanded . . . *brazieri* Hartman
- Reflexed portion of lip white, lip broadly expanded . . . . . 8
8. Spire short, last whorl broadly expanded, umbilicus widely open . . *peasei* (Cox)
- Spire more elongate, umbilicus less widely open . . . . . *delautouri* Hartman

### Genus *Placostylus* Beck, 1837

*Type species*.—*Placostylus bootis* Menke (emended), which has been subsequently restricted to the New Caledonian *Limax fibratus* Martyn, 1789 (see Pilsbry, 1900c, p. 19).

*Remarks*.—Although Martyn's work has been rejected for use in nomenclature (Opinion 456 of the International Commission on Zoological Nomenclature), an effort is being made to conserve many of his names. The nomenclatural status of a New Caledonian species is outside the scope of this study and Martyn's name is quoted above, although it may be nomenclaturally replaced at a later date.

Species assigned to *Placostylus* (sens. lat.) are known from the Solomon Islands south of Bougainville, the Santa Cruz group, the New Hebrides, the Fijis exclusive of the Lau Archipelago, New Caledonia and the Loyalty Islands, Lord Howe Island, and the tip of North Island in New Zealand (figs. 15, 20). Hedley (1898, p. 97) described a "*Placostylus*" from New Guinea, but the relationships of this species are very uncertain (see Iredale, 1941, p. 64). No *Placostylus*, living or fossil, has ever been reported from Australia, Indonesia, or the Pacific Islands west of the Fijis.

Because of their large size and striking coloration, specimens of *Placostylus* are great favorites with shell collectors. Individual shells vary greatly and, like stamp collectors, shell collectors want "new" kinds. As a result, nearly every morphological variation in *Placostylus* has been called a species, and the literature abounds with names

of little or no taxonomic significance. Crosse, Kobelt, Hedley, and Pilsbry attempted to untangle the nomenclatural chaos, but much work needs to be done. In this study several unsorted series of New Hebridean *Placostylus* were available. The range of variation found in these series is so great that I have synonymized most of the New Hebridean "species." Union of several obviously "distinct" species will seem erroneous to some, so the variation is very fully illustrated (pls. 17-22). In the past, too many species have been described on the basis of one or two individuals, and no consideration has been given to the possibility of variation.

It is possible that field studies will demonstrate the presence of local, morphologically stable populations which correspond to some of the "species" here suppressed. The available evidence suggests that the variation is intrapopulational, rather than between populations, but more data are needed. In New Zealand (Powell, 1947, 1951) and New Caledonia (Pain, 1955) local "subspecies" of *Placostylus* have been described, but recognition of similar situations in Melanesia must await detailed field studies. The theoretical implications of the variation in *Placostylus* are discussed above (p. 24).

Not only the variation between specimens but the contrast between arboreal and terrestrial species in *one* archipelago and the differences between species from *different* archipelagos have resulted in the proposal of several subgeneric and sectional names. The earlier ones are listed in Pilsbry (1900c, p. 19); others have been proposed by Iredale (1927), Haas (1935), and Clench (1941). All the names are based on characters of the shell and often indicate the adaptive differences between terrestrial and arboreal species. While they are useful as a means of recognizing species groups within island chains, they fail to show the phyletic relationships of species found in different archipelagos.

Characters of possible value in determining phylogenies do exist, but more study is needed before a definitive classification can be established. Haas (1935) was the first to recognize the importance of embryonic sculpture in classification, and it is apparent that, as in the South American Bulimulidae, there are several kinds of sculpture. *Diplomorpha* (sens. str.) has "wrinkle-striate" sculpture (Pilsbry, 1900c, pl. 72, fig. 17) as do the Santa Cruz and New Hebridean *Placostylus* and the New Zealand and Lord Howe Island species that Haas (1935, p. 188, fig. 3) placed in *Maoristylus*. The New Hebridean *Diplomorpha* (*Quiros*) (see Haas, 1935, p. 190, fig. 1) and New Zealand *Basileostylus* (loc. cit., fig. 4) have longitudinal striae. New

Caledonian species (loc. cit., fig. 1) are finely, densely, and irregularly punctate, while Solomon Island (Pilsbry, 1900c, pl. 72, fig. 18) and Fijian species have regularly spaced, prominent punctations. Pilsbry (1900c, pp. 1-2) considered the striate pattern primitive and the "pitted" sculpture the most advanced. Therefore the Santa Cruz Islands and the New Hebrides, Lord Howe Island, and New Zealand have primitive species; the Solomon and Fiji Islands have advanced species; and the New Caledonian *Placostylus* are only slightly less advanced than the Solomon and Fijian taxa. The New Hebridean and New Caledonian species are totally unrelated.

Pilsbry (1900c), I. and B. Rensch (1935), and Kondo (1948) illustrated the genital anatomy of several species of *Placostylus*, but their results have not been correlated. Only a few species have been dissected, but the trends in the organs of the genitalia parallel those found in the apical sculpture of the shell. *Diplomorpha* has a long spermatheca and a long, slender penis with one large pilaster (see Kondo, 1948), which is the condition found in the primitive South American Bulimulinae and Australian *Bothriembryon*. Both the Santa Cruz Island (see p. 132) and New Zealand (Pilsbry, 1900c) *Placostylus* have similar penial structure but possess shortened spermathecae. P. Fischer (1871) published crude figures of the genitalia of two New Caledonian *Placostylus*, but the internal structure of the penis is not shown. Apparently the New Caledonian species have a very short penis and a medium length spermatheca. In the Solomon Island (I. and B. Rensch, 1935; Kondo, 1948) and Fijian (Kondo, 1948) *Placostylus*, both penes and spermathecae are greatly shortened and the penis is greatly modified internally.

A long spermatheca, a long unspecialized penis, and wrinkled apical shell sculpture seem to be the "primitive" condition, while a short spermatheca, a short specialized penis, and pitted apical shell sculpture might be considered "advanced" characters.

Before a reclassification of the Placostyliinae can be presented, the Lord Howe, New Caledonian, and New Zealand *Placostylus* will have to be dissected. Even with the limited information available, however, certain tentative conclusions can be reached. In the New Hebrides, New Caledonian, Solomon Island and Fijian *Placostylus*, arboreal species are more closely related to terrestrial species from the same area than to arboreal species from another island group. The terrestrial and arboreal species of any one island area have come from the same ancestral stock, that is, there has probably been eco-



logical speciation. Similar situations are found in the zonitid genus *Trochomorpha* (p. 112).

*Diplomorpha* seems to be the most primitive, and the New Hebridean and Santa Cruz *Placostylus* can be easily derived from a *Diplomorpha*-like ancestor. The New Hebrides have the most primitive Placostylineae, and, in *Quiros*, the type which is probably nearest the South American Bulimulinae. The anatomical differences between *Diplomorpha* and the Santa Cruz *Placostylus* are not very significant, and without the obvious conchological differences generic separation would not be advisable. The New Zealand and Lord Howe Island *Placostylus* are quite similar to the New Hebridean species. Until the anatomy has been studied, the exact degree of relationship will remain unknown, but on the basis of apical sculpture not even sectional separation is justified. The New Caledonian species of *Placostylus* have a completely different apical sculpture. Although the anatomical structures are still unstudied, probably subgeneric or generic separation of the New Caledonian from the New Hebridean species will be justified. The Solomon Island and Fijian species have shell sculpture and anatomical features very different from those of the New Hebridean *Placostylus*, but they appear to be closely related to each other. These tentative relationships are shown (fig. 5).

A formal classification based on the relationships suggested here is not presented at this time, but the phylogenetic ideas are used in discussing the zoogeography of the Pacific land snails. Hedley (1892a, 1898, 1899) postulated a former Melanesian continent embracing the area from New Guinea to the Fijis and New Zealand. This area of land connections, even if it did not form a continuous mass, was subject to sufficient fluctuations to allow essentially dry land passage of the placostyline shells. Hedley (1892a) suggested an Indonesian derivation, but later (1899), recognizing the affinities with the South American Bulimulidae, he proposed an Antarctic migration in Mesozoic or Paleozoic times. This view was adopted by Pilsbry (1900c, 1911) and several other authors. In the zoogeographical survey (p. 327) it is suggested that less difficulties are encountered if a northern origin is postulated for the Placostylineae.

The New Hebridean species of *Placostylus* have been placed in two sections, one containing the arboreal, the other the terrestrial species. The terrestrial species, *P. hullianus* (Iredale), *P. salomonis* (Pfeiffer), and *P. fuliginus* (Pfeiffer), are in the section *Santacharis*; the arboreal species, *P. bicolor* (Hartman) and *P. turneri* (Pfeiffer), are in the section *Poecilocharis*. The apical sculpture of the species is

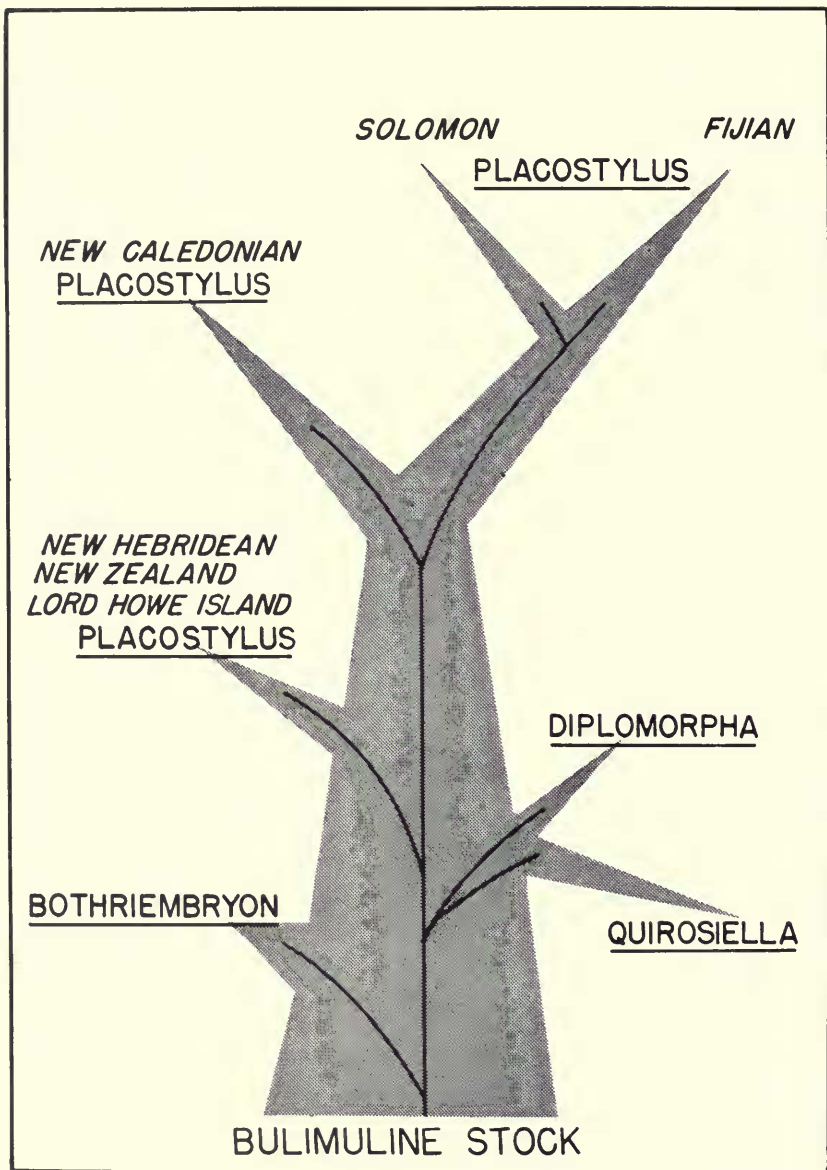


FIG. 5. Phylogeny of the Pacific Bulimulidae.

identical and the sectional names will probably be dropped when the anatomy has been studied. They are convenient indicators of the habitat and have been retained, but not characterized, pending further study.

There are literature records for several *Placostylus* which are not actually found in the New Hebrides. *Placostylus cuniculinsulae* and *P. bivaricosus* are found only on Lord Howe Island off Australia (Iredale, 1944) and not in the New Hebrides (see Kobelt, 1881). *Placostylus stutchburyi* and *P. palmarum* are common in the Solomon Islands (see Clench, 1941) but the specimens in museums labeled "New Hebrides" (UMMZ 816, UMMZ 13891) are from the Cuming collection, which is notorious for its erroneous data. The "*Bulimus janus*" of Kobelt (1881) is an *Amphidromus* from Burma and Mergui (see Pilsbry, 1900c, p. 156).

#### Section SANTACHARIS Iredale, 1927

*Type species.*—*Santacharis hullianus* Iredale.

*Remarks.*—Variation within the terrestrial species, *P. hullianus*, *P. fuliginosus*, and *P. salomonis*, is large and only study of series of specimens clearly reveals the patterns. All three species show clinal variations from slender to obese, smooth to rugose, unicolorous to streaked, flaring to indented lip, white to orange-colored aperture, strong to weak columellar sinus, and dark to light ground color. The named varieties are combinations selected from these independent clinal gradients. Population studies may demonstrate the existence of local morphologic races, but the available material suggests that there has been extensive phyllosynapsis between local populations (see Hubbell, 1956).

*P. fuliginosus* can be easily separated from the other two species by its completely closed umbilical chink, although in a few specimens of *P. salomonis* (pl. 19, figs. 5–8) the umbilicus is rimate rather than open. The affinities of *P. salomonis* and *P. hullianus* are less clear, but the difference in apical sculpture probably is indicative of specific separation.

#### **Placostylus (Santacharis) hullianus** (Iredale). Plate 18, fig. 8.

*Santacharis hullianus* Iredale, 1927, Rec. Australian Mus., 16, (1), p. 77, pl. 5, fig. 1—Santa Cruz Island.

*Santacharis hullianus expeditionis* Iredale, 1927, Rec. Australian Mus., 16, (1), p. 77, pl. 5, fig. 2—Carlisle Bay, Santa Cruz Island.

*Placostylus (Santacharis) salomonis odhneri* Jaeckel and Schlesch, 1952, Jour. de Conchy., **92**, (4), p. 156, pl. 6, fig. 3—Santa Cruz Island; Watson, 1953, Jour. de Conchy., **93**, (3), p. 98.

*Range*.—Santa Cruz Island.

*Material*.—Santa Cruz Island (AMNH).

*Remarks*.—The original descriptions and illustrations of *P. hullianus*, *expeditionis*, and *odhneri* show the kinds of variations found in specimens of *P. salomonis*. No adults from Santa Cruz Island were available, but R. H. Beck collected two lots of juveniles in February, 1927, one from 300 feet elevation, the other from 1000–2000 feet. The specimens from the lower altitude have a more elongate spire, thus paralleling the postulated situation in *P. bicolor* (see p. 137). The spire of *P. hullianus* is more swollen than that of *P. salomonis* and the apical sculpture more prominent (10 ridges/mm. in *hullianus*; 18/mm. in *salomonis*). Probably *expeditionis* and *odhneri* only represent local populations.

Several juvenile animals were dissected. The terminal portions of the genitalia are shown on Plate 6. Although the specimens are not fully mature, a few comparisons with *Diplomorpha* (Kondo, 1948, pl. 8, and specimens from Omba) can be made. *P. hullianus* has a shorter, broader penis, longer vagina, and shorter spermatheca, but the internal structure of the penis is the same as in *Diplomorpha*. Both *Diplomorpha* and *P. hullianus* have a single long, rugose pilaster and no trace of the complicated epiphallic structure found in the Solomon Island and Fijian *Placostylus*.

Iredale (1927, p. 77) reported that the field notes of Troughton and Livingston state that the variety *expeditionis* was found “on leaves.” The shell has all the characteristics of a terrestrial species. Since terrestrial shells are occasionally found on the leaves of bushes and succulents, as were the AMNH shells, Iredale’s conclusion that they were “undoubtedly collected on trees” cannot be accepted.

***Placostylus (Santacharis) salomonis* (Pfeiffer).** Plate 8, figs. 4, 5; plate 17; plate 18, figs. 1–7; plate 19, figs. 5–13.

*Partula salomonis* Pfeiffer, 1852, Proc. Zool. Soc. London, **1852**: 137—Solomon Islands (error); Pfeiffer, 1855, Conch. Cab., I, (13), p. 276, pl. 66, figs. 10, 11; Dohrn, 1862, Malak. Blätt., **9**: 213—identity of *pyrostomus* and *salomonis*.

*Bulimus pyrostomus* Pfeiffer, 1860, Proc. Zool. Soc. London, **1860**: 137—Erromanga; Brazier, 1890, Jour. of Conch., **6**: 79.

*Bulimus salomonis* Pfeiffer, Crosse, 1864, Jour. de Conchy., **12**: 131–133, pl. 7, fig. 8.

*Placostylus pyrostomus* Pfeiffer, Kobelt, 1891, Conch. Cab., I, (13a), p. 68, pl. 16, figs. 5-8.

*Placostylus salomonis* Pfeiffer, Pilsbry, Man. Conch., (2), 13: 69-70, pl. 6, figs. 6-9.

*Range*.—Erromanga, Aneiteum, Tanna, Futuna(?), Espiritu Santo(?).

*Material*.—Erromanga (AMNH); Aneiteum (AMNH); Tanna (USNM 99692, ex LeGrand; photograph from BM collected by MacGillivray in 1854); ?Futuna (AMNH, juvenile); New Hebrides (UMMZ 146861, ex Walker, Tomlin; CM 62.2855, ex Hartman); photograph of holotype of *pyrostomus* (BM).

*Remarks*.—The identity of *salomonis* and *pyrostomus* was established as far back as 1862. Many have preferred to use the later name *pyrostomus* because of the "misleading" nature of the term *salomonis* for a New Hebridean species. Brazier (loc. cit.) reported both *P. fuliginus* and *P. salomonis* from Aneiteum and this is confirmed by the material (AMNH). *P. salomonis* is also known from Terebu, Espiritu Santo (Sykes, 1903, p. 197).

The holotype of *pyrostomus* (pl. 8, fig. 5) is more slender than most of the specimens seen, but it is not too atypical. The holotype of *salomonis* could not be located in the British Museum. Both "species" were probably collected on Erromanga.

Eighteen of the thirty specimens seen were found on Aneiteum and Erromanga by L. Macmillan in 1937 (AMNH collection). The wide range of variation in obesity, spire-aperture ratio, degree of closure of umbilical chink, extent of columellar sinus, shape of aperture, prominence of parietal and columellar callus, and extent of surface sculpture is illustrated (pls. 17, 18). All of the above characters have been utilized in determining "specific" differences.

Specimens from Tanna (pl. 8, fig. 4) are of both the elongate and the globose varieties. Juvenile shells from Futuna Island (AMNH) have the apical sculpture of *P. salomonis* but are too young for positive specific identification.

*P. salomonis* differs from *P. fuliginus* in being generally more obese and lighter in color and in always having an open umbilical chink. Color patterns and sculpture overlap, although *P. fuliginus* is usually darker and more heavily malleated. The orange lip color mentioned by Jaeckel and Schlesch (1952, p. 156) is more often absent than present.

*P. salomonis* lives "under tufts of grass . . . in the mountain ranges of Aneiteum." (Brazier, 1890, p. 79.) No other ecological information is available.

**Placostylus (Santacharis) fuliginus** (Pfeiffer). Plate 8, figs. 3, 6; plate 19, figs. 1-4; plate 20; plate 21, figs. 1-6.

*Bulimus fuliginus* Pfeiffer, 1852, Proc. Zool. Soc. London, 1852: 85—New Hebrides; Pfeiffer, 1854, Conch. Cab., I, (13), p. 157, pl. 48, figs. 5-6; Crosse, 1864, Jour. de Conchy., 12: 129, pl. 7, fig. 4; Brazier, 1890, Jour. of Conch., 6: 80.

*Bulimus fuliginus* var. *beta* Pfeiffer, 1859, Monog. Helic. viv., 4: 363—Aneiteum (MacGillivray).

*Placostylus fuliginus* Pfeiffer, Kobelt, 1891, Conch. Cab., I, (13a), pp. 44-46, pl. 10, figs. 5-8, pp. 74-75, pl. 17, fig. 8(?); Pilsbry, 1900, Man. Conch., (2), 13: 70-71, pl. 11, figs. 2-4, pl. 14, figs. 9-12.

*Placostylus alienus* Pilsbry, 1893, Nautilus, 6: 116-117—New Hebrides; Pilsbry, 1900, Man. Conch., (2), 13: 72-73, pl. 8, figs. 18-19.

*Placostylus heterostylus* Pilsbry, 1900, Man. Conch., (2), 13: 72, pl. 7, figs. 11-12—New Hebrides.

*Range*.—Aneiteum and Erromanga.

*Material*.—Aneiteum (AMNH; USNM 23017, Geddie; ANSP 4883, ex A. Brown, Cox; ANSP 8365, ex A. Brown; CM 62.2856, ex Hartman); Erromanga (AMNH); New Hebrides (UMMZ 13890; UMMZ 146811, ex Walker, Ford; UMMZ 146812, ex Walker, Wetherby; ANSP 8364, holotype of *heterostylus*, ex Swift, Bland; ANSP 62431, holotype of *alienus*, ex Cox).

*Remarks*.—*P. fuliginus* has the same variations in obesity, spire-aperture ratio, columellar sinus and callus, color, sculpture and apertural shape that are found in the other species. In some specimens there is a strong columellar cord (see pl. 20, figs. 6-8). Pilsbry's species, *alienus* and *heterostylus*, were based on single specimens and represented accentuated development of several clinal gradients. Without the series collected by Macmillan they would have been considered distinct. *P. alienus* (ANSP 62431, pl. 21, fig. 5) is small and has a very strong columellar cord and callus, the outer lip is slightly indented and there is no columellar sinus. *P. heterostylus* (pl. 20, fig. 3) is smooth, light-colored, and obese, with a wide, flaring aperture, a thin parietal callus and a slightly sinuate columella. The type locality of these two forms is here restricted to Aneiteum. The typical variety of Pfeiffer (pl. 8, fig. 6, courtesy of BM) is a dark, rather squat and obese, heavily malleated shell. The variety *beta* (pl. 8, fig. 3, courtesy of BM), figured by Kobelt (loc. cit., pl. 17,

fig. 8) is the slender, elongate shell commonly seen in collections. It must be emphasized that these named varieties are not constant—that each specimen presents a different combination of characters selected from the several clinal gradients. On the basis of conchological characteristics, each specimen could be called a different variety.

Previously *P. fuliginus* was reported only from Aneiteum, but one specimen of *fuliginus* was found in a lot of *salomonis* from Erromanga (AMNH). A single specimen of *salomonis* was in the lot of *fuliginus* from Aneiteum. Brazier (1890, pp. 79–80) reported finding both *P. fuliginus* and *P. salomonis* together under clumps of grass on Aneiteum. Field studies are needed to verify the occurrence of both species on Aneiteum and Erromanga and to establish their ecologic relationship.

Table VII.—Size Variation in *Placostylus salomonis* and *Placostylus fuliginus*

|               | <i>P. salomonis</i><br>(16 specimens) |      |      | <i>P. fuliginus</i><br>(17 specimens) |      |      |
|---------------|---------------------------------------|------|------|---------------------------------------|------|------|
|               | Range                                 | Mean | S.D. | Range                                 | Mean | S.D. |
| Height.....   | 36.8–43.2                             | 39.3 | 2.07 | 33.7–40.9                             | 37.1 | 1.99 |
| Diameter..... | 20.6–24.0                             | 22.5 | 0.98 | 17.6–20.3                             | 19.2 | 0.68 |
| H/D.....      | 1.60–1.97                             | 1.74 | 0.12 | 1.77–2.16                             | 1.94 | 0.07 |
| Spire.....    | 12.6–21.7                             | 15.7 | 2.22 | 13.3–18.1                             | 15.9 | 1.50 |
| Aperture..... | 21.3–26.0                             | 23.6 | 1.37 | 19.1–23.0                             | 21.1 | 1.03 |
| S/A.....      | 0.51–0.99                             | 0.67 | 0.12 | 0.60–0.88                             | 0.76 | 0.07 |

A morphometric table (Table VII) comparing *P. fuliginus* and *P. salomonis* is based solely on material collected in 1937 (AMNH). Inclusion of other lots affected mainly the range and lessened the value of this table as a comparison of two simultaneously sampled populations. The major difference between *P. salomonis* and *P. fuliginus* lies in diameter; 94 per cent of all observed specimens of *P. fuliginus* were less than 21 mm. and 94 per cent of all observed specimens of *P. salomonis* were more than 21 mm. in diameter.

#### Section POECILOCHARIS Kobelt, 1891

*Type species.*—*Placostylus hartmanni* Kobelt (= *bicolor* Hartman).

*Placostylus bicolor* (Hartman) and *P. turneri* (Pfeiffer) are arboreal species closely allied to *Santacharis*. The apical sculpture is the same in *Santacharis* and *Poecilocharis*, while the thinner shell, brighter color, and larger aperture of *Poecilocharis* are correlated with the arboreal habitat. *P. turneri* differs from *P. bicolor* in having a much larger aperture, a less reflexed and thicker lip, and an imperforate umbilicus.

**Placostylus (Poecilocharis) bicolor** (Hartman). Plate 12, figs. 6–9; plate 22.

*Charis bicolor* Hartman, 1889, Proc. Acad. Nat. Sci. Philadelphia, 1889: 91, pl. 5, figs. 1, 1a—Aore Island.

*Charis rossiteri* Hartman, 1889, Proc. Acad. Nat. Sci. Philadelphia, 1889: 91, pl. 5, figs. 2, 2a (not *Bulimus rossiteri* Brazier, 1881).

*Placostylus (Poecilocharis) hartmanni* (sic) Kobelt, 1891, Conch. Cab., I, (13a), p. 78, pl. 18, figs. 7–9—new name for *rossiteri* Hartman.

*Placostylus (Charis) bicolor* Hartman, Kobelt, 1891, Conch. Cab., I, (13a), p. 81, pl. 19, figs. 5, 6.

*Placostylus francoisi* Mabille, 1895, Bull. Soc. d'Hist. Nat. d'Autun, 8: 410—Espiritu Santo; Pilsbry, 1900, Man. Conch., (2), 13: 74–75; Ancy, 1905, Nautilus, 19: 44.

*Placostylus hebridarum* Mabille, 1895, Bull. Soc. d'Hist. Nat. d'Autun, 8: 410—Espiritu Santo; Pilsbry, 1900, Man. Conch., (2), 13: 75–76.

*Placostylus (Poecilocharis) hartmani* Pilsbry, 1900, Man. Conch., (2), 13: 73–74, pl. 45, figs. 8–12—emendation of Kobelt's misspelling.

*Placostylus (Poecilocharis) bicolor* (Hartman), Pilsbry, 1900, Man. Conch., (2), 13: 74, frontispiece, figs. 1–4.

*Range*.—Espiritu Santo and Aore Islands.

*Material*.—ML 33, ML 76, NH 2; Hog Harbour (MCZ 132314); holotypes of *rossiteri* Hartman (= *hartmanni* Kobelt) (ANSP 60067) and *bicolor* Hartman (CM 62.4683), Second Channel, Espiritu Santo (CM 62.2885, ex Hartman, Layard); New Hebrides (MCZ 102017, ex Bequaert).

*Remarks*.—Specimens which are intergrades between *hartmanni* and *bicolor* are illustrated (pl. 22). The greater obesity (lower spire) of *bicolor* is probably correlated with altitude and is not taxonomically significant. *P. francoisi* Mabille (pl. 12, figs. 8, 9) and *P. hebridarum* Mabille (pl. 12, figs. 6, 7) are within the range of variation shown by the Kuntz material and are here synonymized.

*P. bicolor* has a dimorphic color pattern, typified by the “varieties” *francoisi* and *hebridarum*. In the former, longitudinal streaks predominate, in the latter, spiral bands. The epidermal color pattern is formed by the deposition of waste products as pigments (Comfort, 1951). Spurts of shell growth might conceivably result in a streaked pattern, while slow continuous growth would emphasize the spiral pattern. Underneath the epidermal color pattern is a ground color which consists of a saffron spire fading to white on the body whorl (see Pilsbry, 1900c).

The type localities cited by Hartman are questionable. An original label with *bicolor* reads “Santo Is., near Aure (= Aore) Island”



and a partly decipherable note with the holotype of *rossiteri* indicates that it was collected on "Segon or Saigon on Santo Is. near Aura." Probably Segond Channel on Espiritu Santo is the type locality. All available specimens of typical *bicolor* are worn and without epidermis. If they were collected on Espiritu Santo, they undoubtedly were found near the coast and probably near a river or stream.<sup>1</sup> It would then be quite possible that the shells had been washed down from the interior of the island. This would not mean that *bicolor* and *hartmanni* are distinct, since altitudinally correlated variation is well known in land mollusks (see A. P. Brown, 1911; Pelseener, 1920; van der Schalie, 1948; Solem, 1955) and is found in the New Hebridean *Diplomorpha* (see pp. 140, 141, 143).

**Placostylus (Poecilocharis) turneri** (Pfeiffer). Plate 8, figs. 1, 2.

*Bulimus turneri* Pfeiffer, 1860, Proc. Zool. Soc. London, 1860: 138, pl. 51, fig. 10—Erromanga (Turner).

*Placostylus (Poecilocharis) turneri* Pfeiffer, Pilsbry, 1900, Man. Conch., (2), 13: 75, pl. 45, fig. 5.

*Range*.—Erromanga.

*Material*.—Photograph of holotype (BM).

*Remarks*.—*Placostylus turneri* was listed for exchange by Cox (1868), but I could locate no specimens. It is closely allied to *bicolor*, but has an imperforate umbilicus and a larger aperture. The color pattern is similar to *P. bicolor* var. *hebridarum*.

Genus **DIPLOMORPHA** Ancy, 1884

Shell small, elongate conic to ovate, umbilicate or rimate, solid, whorls  $3\frac{1}{2}$  to  $5\frac{1}{2}$ . Apical whorls  $1\frac{1}{2}$ , with longitudinal striae or wrinkle-striate when not eroded. Cuticle thin, brown. Aperture ovate, peristome thickened or reflexed, usually stained with orange or red. (Adapted from Pilsbry, 1900c, p. 114.)

*Type species*.—*Diplomorpha layardi* Ancy.

*Remarks*.—Early authors such as Kobelt and Ancy considered that *Diplomorpha* represented an intermediate stage between *Placostylus* and *Partula*. The wide anatomical divergence between the latter two became known in the 1890's, but the affinities of *Diplomorpha* remained uncertain until Kondo (1948) demonstrated its close relationship to *Placostylus*. In several respects *Diplomorpha* is more primitive. The long spermatheca inserted near the atrium

<sup>1</sup> Except for J. R. Baker (see p. 13), no person has collected shells from the interior of Espiritu Santo. All known collections were made near the sea coast or from the banks of a stream not more than four miles inland.

and the long slender penis are much nearer the corresponding structures of the South American Bulimulidae than those of the specialized *Placostylus* of the Solomons and Fiji (see Kondo, 1948). The apical sculpture of *Diplomorpha*, consisting of longitudinal striae in *Quiros*, new subgenus, and the wrinkle-striate type in *Diplomorpha* (sens. str.) are more primitive than the pitted sculpture of the New Caledonian, Fijian, and Solomon Island *Placostylus*.

Apparently *Diplomorpha* is restricted to the New Hebrides. Several species, erroneously described from the Solomon Islands, have later been found in the New Hebrides. No *Diplomorpha* have been found on other island groups.

Twelve names are available in *Diplomorpha*, of which perhaps four are entitled to specific rank. One of these, *Diplomorpha bernieri*, is here placed in a new subgenus, *Quiros*. The other three are the toothed *D. layardi* from Vate, *D. coxi* from Aneiteum(?), and the closely related *D. peasei-delaoutouri-brazieri* from Espiritu Santo and Omba Islands. The latter three names probably refer to variants of the same species.

There is a prior generic name of nearly identical spelling, *Diplomorphus* Giraud, 1871 (Ann. Soc. Ent. France, (5), 1: 409). Under present rules of zoological nomenclature, Ancey's genus is not affected. If future changes in the rules should invalidate Ancey's name, *Hebridaria* Pilsbry (1900c, p. 115) has been made available as a replacement.

### Subgenus DIPLOMORPHA

Shell ovate, whorls  $3\frac{1}{2}$  to  $4\frac{3}{4}$ , spire-aperture ratio less than 0.85, surface without longitudinal folds and plications, suture never crenulate. Apical sculpture wrinkle striate, as in *Santacharis*.

*Type species.*—*Diplomorpha layardi* Ancey.

### *Diplomorpha* (*Diplomorpha*) *layardi* Ancey. Plate 23, figs. 7–12.

*Diplomorpha layardi* "Brazier" Ancey, 1884, Il Naturaliste Siciliano, 3: 344—generic description.

*Partula layardi* "Brazier" Hartman, 1885, Proc. Acad. Nat. Sci. Philadelphia, 1885: 223—observations, but not description, of the species.

*Partula* (*Diplomorpha*) *layardi* "Brazier" Hartman, 1886, op. cit., p. 35, pl. 2, fig. 18—figure, but no description.

*Diplomorpha layardi* "Brazier," var. *alticola* Ancey, 1889, Le Naturaliste, 1889, p. 266—" . . . une haute montagne, Vate" (Mt. MacDonald?).

*Partula layardi* Brazier, 1890, Jour. of Conch., 6: 80—Tuker Tuker, Vate or Sandwich Island (no description or figure).

*Partula layardi* var. *alba* Brazier, 1890, op. cit., p. 80—described without locality.

*Placostylus (Diplomorpha) layardi* ("Brazier," Hartman), Pilsbry, 1900, Man. Conch., (2), 13: 115-116, pl. 72, figs. 1-5, 17—described and figured.

*Range*.—Vate Island.

*Material*.—Vila, Vate (CM 62.5291, J. Jetschin, Dec. 1904; Miller 548; UMMZ 146731, ex Walker, Tomlin; ANSP 133293, ex Froggatt); 2,000 feet up, Vate (UMMZ 183209, ex Walker, Ponsonby); Vate (MCZ 180554, ex Shackelford, Tomlin; ANSP 8338, ex Hartman; USNM 603091, var. *alba* ex Higgins, ?Brazier; USNM 603092, ex Higgins, ?Brazier; ANSP 8336, ex Dupuy; MCZ 10209, ex Winkley; CM 62.4676, ex Hartman, Layard); "Salisboe Is." (USNM 56322, error by Hartman in locality); New Hebrides (UMMZ 14045; ANSP 8337, ex Garrett; MCZ 102018, ex Boston Soc. Nat. Hist., Roper; MCZ, ex Bequaert; MCZ 152750, ex Putzeys; MCZ 194761, ex Archer, Fulton).

*Remarks*.—Brazier never published the name *layardi*, which must date from Ancey's description of *Diplomorpha* in 1884. Under Opinion 43 of the International Commission of Zoological Nomenclature, Ancey's usage is equivalent to the term "new genus, new species" of modern systematics. Since Ancey never considered that he described *D. layardi*, it is certain that no specimens labeled "types" are extant.

The presence of named varieties, *alticola* Ancey and *alba* Brazier, necessitated selection of a neotype for the nominate variety. For this purpose, ANSP 8336 (pl. 23, fig. 10) is designated neotype. The shell has been previously figured by Pilsbry (1900c, pl. 72, fig. 2) and, although darker in coloration and less elongate than many specimens, is nevertheless representative of the original specimens sent to Layard by several collectors.

Information on the ecology and type locality of *D. l. layardi* is contained in letters with the Hartman correspondence (CM). In a letter to Brazier, Layard indicated that *D. layardi* was not collected at "Tuker-Tuker (Ford's place), it came first from 'Rathmor' and then the fine large spms. from 'Seaview,' both properties of W. Glisson who discovered it on Vate." The exact localities of Rathmor and Seaview are unknown to me, but probably they are near Havannah Harbour. The type locality is restricted to Rathmor, where it was first collected, and the site of the smaller specimens of which the neotype is representative. A letter from Layard to Garrett is here quoted at length: "As far as I know it [*D. layardi*] is only found on the elevated land at a distance from the coast. They were got at

Seaview (his place) 3 miles from the coast at an elevation of about 1500 feet. It does not seem to move about in the day time, or in dry weather, but remains under dead leaves on which, I think, it feeds. It has not been seen to travel up bushes or trees or attach itself to their leaves. After rain, or when the ground is very moist, it moves about vigorously. As yet I but know it from Vate or Sandwich Island, and they don't seem to have a *Bulimus* [= *Placostylus*] there, though they have another *Partula* . . . which is also found on SW of Aneiteum."

Apparently this is a quotation from a letter sent to Layard by W. Glisson. Brazier (1890, p. 80) reported that *D. layardi* is found under sticks and leaves.

Very few of the forty-seven available specimens had precise locality data. ANSP 133293, from near Vila, represented a population of large, thin, obese shells (pl. 23, figs. 11, 12) which are bright orange in color and have a very small parietal tooth. Miller 548 came from the banks of a small stream about two miles north of Vila. The specimens are smaller, slightly less obese, and darker in color, with a larger parietal tooth. In comparison, the neotype and Hartman's shells (pl. 23, figs. 7, 10) are very solid, somewhat stunted, and dark in color. UMMZ 146731 represented a mixed lot. One label read "Port Vila" (ex Tomlin); the other "2,000 feet up, Vate" (ex John Ponsonby). The mixed lot can be divided into two series corresponding to typical *layardi* and variety *alticola*. The latter were catalogued as UMMZ 183209 with the locality "2,000 feet up, Vate."

I did not see var. *alba* Brazier. The only specimen labeled "*alba*" (USNM 603091, ex Higgins) was an albino *alticola*. The type of *alba* is somewhere in England (Brazier, 1890, p. 66).

Variety *alticola* Ancey (pl. 23, figs. 8, 9) has an elongate spire, and specimens are usually much lighter in color than typical *D. layardi*. The type locality of *alticola* is here restricted to Mount MacDonald,

Table VIII.—Size Variation in *Diplomorpha layardi*

|                    | <i>D. layardi</i> |      |      | <i>D. layardi</i> var. <i>alticola</i> |      |
|--------------------|-------------------|------|------|--|------|
|                    | Range             | Mean | S.D. | Range                                  | Mean |
| Height . . . . .   | 18.9-24.4         | 21.0 | 1.29 | 23.2-25.4                              | 24.2 |
| Diameter . . . . . | 11.9-16.5         | 14.3 | 1.06 | 14.5-16.0                              | 1.63 |
| H/D . . . . .      | 1.33-1.59         | 1.48 | 0.05 | 1.48-1.75                              | 1.63 |
| Aperture . . . . . | 12.3-16.4         | 14.1 | 1.06 | 14.4-16.1                              | 15.2 |
| Spire . . . . .    | 5.5-8.0           | 6.9  | 0.52 | 8.5-9.5                                | 9.0  |
| S/A . . . . .      | 0.38-0.61         | 0.50 | 0.05 | 0.56-0.61                              | 0.59 |
| Whorls . . . . .   | 3½-4              | 3¾   | .... | 4                                      | 4    |

Vate Island. *D. l.* var. *alticola* would be considered a geographic subspecies by many, but the higher spire in mountain forms is such a common adaptation that nomenclatural recognition only serves to burden the literature. The variation in the columellar tooth (pl. 23, figs. 7-12) is potentially of much more evolutionary significance than the variation in height of spire, and *alticola*, although a well-marked form, is not here accepted as a "subspecies."

Several specimens of *D. layardi* collected by Miller have all of the internal partitions of the shell missing. Destruction of the apical whorls and spire by shrew and rodent predation is well known in continental areas, but I know of no predator on snails that will destroy only the internal partitions and not harm the spire.

The variation in forty specimens of *D. layardi* and six of variety *alticola* is summarized in Table VIII.

### Diplomorpha (Diplomorpha) peasei (Cox). Plate 19, fig. 15.

*Partula peasei* Cox, 1871, Proc. Zool. Soc. London, 1871: 644, pl. 52, fig. 2—Solomon Islands (Rainbird!) (error).

*Placostylus (Diplomorpha) peasei* (Cox), Pilsbry, 1900, Man. Conch., (2), 13: 117, pl. 72, figs. 7-9.

Range.—Aore Island(?).

Material.—"Aolia Is." (ANSP 144262).

Table IX.—Size Variation in *Diplomorpha*

|               | Hog Harbour     |                                  |      | <i>D. delautouri</i> |                   |      |
|---------------|-----------------|----------------------------------|------|----------------------|-------------------|------|
|               | Mean            | Range                            | S.D. | Mean                 | Range             | S.D. |
| Height.....   | 22.4            | 20.9-24.6                        | 1.08 | 24.4                 | 20.6-26.9         | 1.15 |
| Diameter..... | 16.3            | 14.1-17.9                        | 0.95 | 17.0                 | 15.2-19.2         | 0.71 |
| H/D.....      | 1.39            | 1.23-1.48                        | 0.07 | 1.44                 | 1.26-1.64         | 0.08 |
| Spire.....    | 9.00            | 8.0-10.1                         | 0.68 | 9.8                  | 8.3-12.3          | 0.94 |
| Aperture..... | 13.3            | 12.2-14.7                        | 0.72 | 14.4                 | 12.3-15.7         | 0.72 |
| S/A.....      | 0.69            | 0.57-0.78                        | 0.05 | 0.69                 | 0.54-0.84         | 0.05 |
| Whorls.....   | 4 $\frac{3}{8}$ | 4 $\frac{1}{8}$ -4 $\frac{3}{4}$ |      | 4 $\frac{3}{8}$      | 4-4 $\frac{3}{4}$ |      |

|               | <i>D. peasei</i> |                   | <i>D. coxi</i>  | <i>D. brazieri</i> |
|---------------|------------------|-------------------|-----------------|--------------------|
|               | Mean             | Range             |                 |                    |
| Height.....   | 21.8             | 20.0-23.7         | 24.5            | 19.0               |
| Diameter..... | 16.3             | 13.2-18.0         | 16.4            | 13.6               |
| H/D.....      | 1.34             | 1.21-1.57         | 1.49            | 1.40               |
| Spire.....    | 8.3              | 7.2-8.7           | 10.3            | 7.6                |
| Aperture..... | 13.5             | 11.5-15.1         | 13.2            | 11.4               |
| S/A.....      | 0.61             | 0.53-0.74         | 0.78            | 0.67               |
| Whorls.....   | 4 $\frac{1}{4}$  | 4-4 $\frac{1}{2}$ | 4 $\frac{3}{8}$ | 4                  |

*Remarks.*—Some years after publishing his review of *Diplomorpha*, Pilsbry received eleven specimens of *D. peasei* from I. S. Oldroyd. The locality is "Aolia Island," which can be taken to be a misspelling of either Aoba (=Omba) or Aore Island. Several specimens of *Partula albescens* were received from the same locality so it is possible that Aore Island was intended. Pilsbry (1900c, p. 117) separated *D. peasei* from *D. delautouri* only by the more open umbilicus (pl. 19, fig. 15) and more expanded body whorl of *peasei*. It is doubtful whether field studies will maintain the separation of the three "species," *delautouri*, *peasei*, and *brazieri*, although a complete series of intergrades could not be found in the available material. A summary of the morphometry of the lot of *D. peasei* (ANSP) is given in Table IX.

***Diplomorpha (Diplomorpha) brazieri* Hartman. Plate 23, fig. 4.**

*Diplomorpha brazieri* Hartman, 1889, Proc. Acad. Nat. Sci. Philadelphia, 1889: 92-93, pl. 5, fig. 6—Aore Island; Ancey, 1905, Nautilus, 19, (4), p. 43—Espiritu Santo.

*Placostylus (Diplomorpha) brazieri* Hartman, Pilsbry, 1900, Man. Conch., (2), 13: 116-117, pl. 72, fig. 6.

*Range.*—Espiritu Santo and Aore.

*Material.*—Aore Island (CM 62.4677 holotype).

*Remarks.*—Hartman stated that all known specimens are worn and without epidermis, but I found only the holotype. The chief characteristics of *D. brazieri* are the narrow orange lip, small size, slender, flat whorls, and non-sinuate peristome. All of these characters vary greatly in *Placostylus*, but not enough is known about *Diplomorpha* to be positive that *brazieri* and *delautouri* are conspecific.

***Diplomorpha (Diplomorpha) delautouri* (Hartman) (emended).**

Plate 19, fig. 14; plate 23, figs. 1-6.

*Partula (Diplomorpha) delatouri* Hartman, 1886, Proc. Acad. Nat. Sci. Philadelphia, 1886: 35, pl. 2, fig. 19—Aore Island, New Hebrides.

*Placostylus (Diplomorpha) delatouri* Hartman, Pilsbry, 1900, Man. Conch., (2), 13: 117-118, pl. 72, figs. 10-12.

*Diplomorpha delantouri* (sic) Hartman, Sykes, 1903, Proc. Malac. Soc. London, 5: 197—Renee River, Espiritu Santo.

*Diplomorpha delantouri* (sic) var. *major* Ancey, 1905, Nautilus, 19, (4), pp. 43-44—Espiritu Santo.

*Range.*—Aore, Omba, and Espiritu Santo.

*Material.*—ML 10, ML 31f, ML 31g, ML 31h, ML 32, ML 33, ML 37, ML 37, ML 39, ML 42, ML 76, ML 90, NH 2; Aore Island (CM 62.4680, ex Hartman, lectotype); Omba (AMNH, Drowne!);

Espiritu Santo (CM 62.4679, ex Hartman); Hog Harbour, Espiritu Santo (MCZ 109445); Segond Channel, Espiritu Santo (UMMZ 146792, ex Walker, Ponsonby, Layard); New Hebrides (MCZ 102019, ex Bequaert; MCZ 10208, ex Winkley).

*Remarks.*—The collector of this species, George de Lautour, was a middle-aged planter later killed by natives and not “an enthusiastic young scientist” (see Rannie, 1912, pp. 151–152). Hartman’s original spelling, *delatouri*, is invalid. Under the present rules of zoological nomenclature (Hemming, 1953, p. 45, paragraph 73) the name, *delautouri*, as a “valid emendation” must date from this author and paper. Such a course is ridiculous, since the species was described by Hartman and the addition of a single letter to the *name* does not change the *species* in any way. The species is quoted hereafter as *Diplomorpha delautouri* Hartman.

The type locality is herein restricted to the portion of Aore Island facing Espiritu Santo (see pl. 2), and CM 62.4680 is selected as the type specimen. Specimens from Aore Island are smaller (19.3–19.7 mm. high) than those from Espiritu Santo (20.6–26.9), and Ancy (1905, p. 44) named the Santo shells var. *major*, based on material in the Paris Museum collected by François (see Mabille, 1895, p. 411). Dwarfed shells on small islands are common in land snails (Pelseneer, 1920, p. 560) and should not be nomenclaturally recognized.

The variation in a lot of seventeen specimens from Hog Harbour (MCZ 109445), in a lot of sixty-five specimens from a road cut in the Sarakata River Valley (ML 33), and in *D. peasei* and *D. brazieri* is summarized in Table IX. The differences between the Hog Harbour and Sarakata River specimens are of the same type as those found between *D. layardi* and *D. layardi* var. *alticola*. The material from ML 33 is a thanatocoenosis of shells deposited by flood waters. Dead land shells with a bubble of air trapped inside the spire are often picked up by flood waters and carried for considerable distances before being deposited and covered by debris. Many of the shells in ML 33 were probably washed down from the mountains and it is quite possible that a high-spired form of *delautouri* inhabits the interior of Espiritu Santo. The direction of the variational trend is opposite in *Placostylus* (higher spire in lowlands) and *Diplomorpha* (higher spire in uplands). Study of the ecology of the two genera may help to explain the mechanism controlling clinal variation in shell height, which is correlated with altitudinal changes.

The variations found in height, peristomal swelling, and degree of lip expansion are illustrated (pl. 23). There was no significant

color variation, all specimens having the streaked shell, orange aperture, and white reflected lip.

Little is known of the ecology of *D. delautouri*. The appearance is that of a terrestrial species, and most of Kuntz's specimens were found under decaying logs, in leaf mould, or under tufts of grass. A few specimens, however, were found on the trunks and limbs of trees from one to seven feet above the ground. Young shells were found in January and early February, and nearly adult specimens in late February and early March. Only adult specimens were collected in October and June. Drowne picked up both adult and very young specimens on Omba in June, 1927.

Kondo (1948, pp. 119-122, pl. 8) studied the anatomy of a single adult specimen. Three juveniles preserved by Kuntz were too young for study, but I dissected several adults obtained by Drowne and they completely confirmed the observations made by Kondo. The anatomy has not been refigured.

### **Diplomorpha (Diplomorpha) coxi** (Pease). Plate 16, fig. 1.

*Bulimus* (?*Borus*) *coxi* Pease, 1871, Amer. Jour. Conch., 7: 197—Solomon Islands (Rainbird) (error).

*Diplomorpha coxi* Hartman, 1891, Proc. Linn. Soc. New South Wales, (2), 6: 571, pl. 21, figs. 1, 3, 6—*Aneiteum*(?).

*Placostylus* (?) *coxi* Pease, Pilsbry, 1900, Man. Conch., (2), 13: 90.

*Placostylus (Diplomorpha) coxiana* Pilsbry, 1900, Man. Conch., (2), 20: 118, pl. 72, figs. 13-14—new name for *P. coxi* Hartman (not Pease).

*Diplomorpha coxi* Pease, Clench, 1932, Nautilus, 46, (2), pp. 68-69, pl. 2, fig. 8.

*Range*.—*Aneiteum*(?).

*Material*.—Solomon Islands (MCZ 86495, holotype of *B. coxi* Pease).

*Remarks*.—The holotype of *D. coxi* (Pease) (MCZ 86495) had been badly broken and then repaired at several different times during the life of the animal. The apical whorls are cracked and have several chips missing, the spire shows signs of at least two minor injuries, the body whorl is badly broken near the columellar wall, and there is another bad break behind the lip. Thus much of the appearance of the holotype can be attributed to former injuries. The spire of *coxi* is wider than in *D. delautouri*, but otherwise the species are quite similar. The relationship to *D. coxi* Hartman is quite uncertain (see Clench, 1932). The illustrations of that species do not allow a close comparison. The spire of Hartman's species is much more produced and narrower than that of Cox's species. The rela-



tionship of the two can only be determined by re-examination of the type of *coxi* Hartman in the Australian Museum. Until then, nothing can be gained by separating the "species." In a letter to Hartman, written in Sydney, Layard indicated that he doubted that Cox's specimen, the holotype of *coxi* Hartman, came from Aneiteum. Both forms may prove to be long-spined forms of *delautouri*.

### QUIROS, new subgenus

Shell elongate, whorls 4½ to 5½, spire-aperture ratio 0.87 or greater, surface with longitudinal folds or plications, sutures crenulate in many specimens. Apical sculpture of widely spaced, parallel longitudinal striae. Anatomy as in *Diplomorpha* (sens. str.).

*Type species*.—*Bulimus bernieri* Hartman.

*Remarks*.—The apical sculpture, elongate form, greater number of whorls and surface sculpture separate *Quiros* from *Diplomorpha* (sens. str.). The apertural shape and color, umbilicus, genital anatomy, and columellar structure are quite similar to *Diplomorpha* (sens. str.) and suggest that *Quiros* be considered a subgenus rather than a genus.

### *Diplomorpha* (*Quiros*) *bernieri* (Hartman). Plate 21, figs. 7, 8.

*Bulimus ruga* Hartman, 1890, Proc. Acad. Nat. Sci. Philadelphia, 1890: 284, pl. 3, fig. 1—Segou Island (=Segond Channel, Espiritu Santo).

*Bulimus bernieri* Hartman, 1890, Proc. Acad. Nat. Sci. Philadelphia, 1890: 284, pl. 3, fig. 2—Segou Island (=Segond Channel, Espiritu Santo).

*Diplomorpha ruga* (Hartman), Ancey, 1897, Nautilus, 11, (3), pp. 26–27.

*Diplomorpha bernieri* (Hartman), Ancey, 1897, Nautilus, 11, (3), pp. 26–27.

*Placostylus* (*Diplomorpha*) *ruga* (Hartman), Pilsbry, 1900, Man. Conch., (2), 13: 119, pl. 72, fig. 15.

*Placostylus* (*Diplomorpha*) *bernieri* (Hartman), Pilsbry, 1900, Man. Conch., (2), 13: 119–120, pl. 72, fig. 16.

*Placostylus* (?) *bernieri* (Hartman), Sykes, 1903, Proc. Malac. Soc. London, 5: 197—Renee River, Espiritu Santo.

*Range*.—Espiritu Santo.

*Material*.—ML 11, ML 33, ML 42, ML 46, ML 76; Segond Channel (ANSP 132670).

*Remarks*.—Hartman's type specimens could not be located. They are not in the Carnegie Museum, and, since Ancey, Kobelt, Sykes, and Haas have examined specimens, the types may be in a European museum. For a long time it was uncertain whether *D. bernieri* was a bulimulid or a partulid, but the roseate aperture and embryonic

Table X.—Size Variation in *Diplomorpha bernieri* (Hartman)

|            | Height    | Diameter  | H/D       | Spire     | Aperture  | S/A       | Whorls |
|------------|-----------|-----------|-----------|-----------|-----------|-----------|--------|
| Mean.....  | 25.2      | 13.6      | 1.85      | 12.7      | 12.6      | 1.02      | 5½     |
| Range..... | 23.7-27.3 | 12.2-14.7 | 1.68-2.08 | 11.2-14.1 | 11.4-13.7 | 0.87-1.18 | 4⅞-5⅝  |
| S.D.....   | 0.97      | 0.60      | 0.09      | 0.40      | 0.38      | 0.06      | ...    |

sculpture (see Haas, 1935, p. 190, fig. 1) are unknown in the Partulidae but are common to both *Placostylus* and *Diplomorpha*.

On the basis of sutural sculpture (pl. 21, figs. 7, 8), two species were originally recognized. Both types of sculpture are often found on the same specimen; thus only one species can be recognized. The name *ruga* has page and line priority, but the name *bernieri* is here selected, as it represents the common variety, and *ruga*, with its "ruffled" suture, is a rather rare variant.

Nothing is known of the ecology of *D. bernieri*. The specimens in lot ML 11 were found on the decaying trunk of a coconut palm, but Commander Kuntz's field notes fail to indicate if they were alive or dead. ML 33 contained many dead shells and the morphometry of 62 adults is summarized in Table X.

### Family PARYPHANTIDAE<sup>1</sup> (= Rhytididae)

Carnivorous agnathomorphous sigmurethra. Shell depressed-globose, planulate, or auriform, umbilicated. *Paryphanta* and *Schizoglossa* have shells with few calcareous elements. Color usually brown or green, shell more or less prominently variegated with reddish-brown. Periphery rounded or keeled. Sculpture of weak spiral lines and/or radial ribs, or smooth. Peristome simple, not reflected or thickened. Animal without peripodial grooves or caudal mucous pore. Mantle not reflected over shell. Jaw absent. Radula with less than 100 rows of teeth; central tooth absent in many species; lateral teeth unicuspid and large. Reproductive system without talon, epiphallic flagellum, dart-sac, or glands. Duct of spermatheca unbranched. Penis with papillae or large stimulatory organ.

The Paryphantidae are found in South Africa, the Seychelles, Indonesia, Melanesia, the Caroline Islands, Samoa, Tonga, New Zealand, and eastern Australia (fig. 18). The only monographic study is by Moellendorff (1903-1904). No general account has appeared since then but the papers of Watson (1934), Connolly (1939), Kondo (1943), and Powell (1930-49) contain much valuable information.

The South African species (see Watson, 1934, and Connolly, 1939) are placed in two genera, *Natalina* and *Nata*. *Natalina* appears to be an analogue of the Austro-Zelandic *Rhytida* and was considered a subgenus of *Rhytida* by Thiele (1931, p. 726). Very probably, *Natalina* and *Rhytida* are only convergent (see Watson, 1934, p. 153), and they are here maintained as distinct genera. The shell of *Nata* is very similar to some Australian *Delos*, but until the anatomy of the latter genus has been fully studied, the exact nature of their relation-

<sup>1</sup> Paryphantinae Godwin-Austen, 1893, antedates Rhytididae Pilsbry, 1895 (see H. B. Baker, 1956a, b), and since both have been used with equal frequency, the law of priority has been followed here.

ship will remain obscure. The South African paryphantids are quite restricted in range, none having been found north of 25° S. Lat. Genera from tropical Africa formerly included in the Paryphantidae are now known to belong elsewhere (Watson, 1934, p. 152).

The relationships of the Pacific paryphantids are very poorly understood. Thiele (1931, pp. 724-726) utilized nine genera and subgenera for all the Pacific species, while Iredale (1933, 1938) created eleven *new* genera for the Australian species alone. In arranging the paryphantids for zoogeographic considerations, I have demoted Iredale's genera to sections or synonyms of previously described taxa. This reclassification indicates the broad lines within the family in regard to shell structure. The anatomy of the paryphantids is too incompletely known to be used in creating a phylogenetic classification, although previous studies (see Kondo, 1943, for references) have shown that numerous characters of value in taxonomy exist in the anatomy. A clearer concept of distribution and conchological relationships can probably be obtained by retention of broad taxonomic categories than by a great proliferation of generic names. For this reason, the Indo-Pacific Paryphantidae have been grouped as follows:

#### GROUP A.

Genus *Paryphanta* Albers, 1850 (type species, *Helix busbyi* Gray).

Section *Powelliphanta* O'Connor, 1945.

Section *Victaphanta* Iredale, 1933.

*Distribution*: New Zealand, Victoria.

Genus *Wainuia* Powell, 1930 (type species, *Helix urnula* Pfeiffer).

*Melavitrina* Iredale, 1933, is doubtfully separable.

*Distribution*: New Zealand, Tasmania.

Genus *Schizoglossa* Hedley, 1892 (type species, *Daudebardia novoseelandica* Pfr.).

*Distribution*: New Zealand.

#### GROUP B.

Genus *Rhytida* Albers, 1860 (type species, *Helix greenwoodi* Gray).

*Distribution*: New Zealand, Tasmania, Australia, New Caledonia.

Genus *Delos* Hutton, 1904 (type species, *Zonites coresia* Gray).

*Distribution*: Rotuma, New Hebrides, New Caledonia, New Zealand, Australia, Caroline Islands.

Genus *Macrocycloides* Martens, 1869 (type species, *Helix arthurii* Pfeiffer).

*Distribution*: Buru, Borneo, Ambon, Saparua, Ceram, Solomon Islands, New Hebrides.

Genus *Ouagapia* Crosse, 1894 (type species, *Helix raynali* Gassies).

*Distribution*: New Caledonia, Solomon Islands, New Guinea, Bismarcks, New Hebrides, Tonga, Samoa, Fijis.

#### GROUP C.

Genus *Diplomphalus* Crosse and Fischer, 1873 (type species, *Helix cabriti* Gassies).

*Distribution*: New Caledonia.

The use of groups "A," "B," and "C" show the major types of conchological variation and do not necessarily reflect phylogeny. The three genera of group "A" have a globose or auriform shell composed mainly of a thick layer of conchin with very few calcareous elements. The animals are too large to retreat into the shell, and the species are restricted to very humid situations. In New Zealand, *Paryphanta* are found in isolated colonies, usually at more than 2,000 feet elevation, and have evolved numerous local forms (Powell, 1930, 1946a, b, 1949). Group "C" contains a few specialized New Caledonian species. Their multi-whorled, flat shell cannot be mistaken for any other paryphantid. The genera in group "B" may be primitive and "A" and "C" specialized offshoots.

Several genera which are sometimes placed in the Paryphantidae need further discussion. *Occirhenea* Iredale, 1933, was proposed for *Helix georgiana* Quoy and Gaimard, 1832, a species from King George Sound, Southwest Australia. Later, Iredale (1939, p. 73) created a new family, the Occirheneidae, for this species. The original illustrations show a helicid type of shell, but determination of its systematic position must await study of the shell and its anatomy. The New Guinean "paryphantid" genera *Gallodema* and *Illonesta* Iredale (1941, p. 94) are endodontids synonymous with *Paryphantopsis* (Thiele, 1928a, pp. 125-126) (see Solem, in press-A).

In his masterly essay on the carnivorous pulmonates, Hugh Watson commented on the past history of the Paryphantidae. The little information appearing since 1915 does not affect his conclusions and the following account has been condensed, with minor alterations, from Watson (1915, pp. 231-256).

As to both distribution and anatomy, the Paryphantidae seem to be the oldest carnivorous family.<sup>1</sup> After an early Mesozoic or late Paleozoic origin, the paryphantids radiated, eventually reaching South Africa, Australia, Melanesia, and New Zealand. It is not

<sup>1</sup> The carnivorous Rathouisiidae belong to a more primitive stock of the Pulmonata, but their distribution suggests that they evolved at a later date than the paryphantids. While they are more primitive, they are also more recent.

known that they ever inhabited South America, but a few genera such as *Guestieria* and *Macrocyclus* could conceivably be aberrant paryphantids. The present distribution of the Paryphantidae can best be understood in relation to the evolution and distribution of some other carnivorous land mollusks.

The Streptaxidae are the common carnivorous mollusks of Africa, South America, and the mainland of Asia. It is quite probable that they evolved from primitive paryphantids. Within the Streptaxidae there have been three lines of evolution: the helicoid, the pupaeform, and the cylindrelloid types of shell. In a few areas, for example, East Africa and the Mascarene Islands, large pupaeform streptaxids have developed, but generally they are small. The pupaeform and cylindrelloid streptaxids are adapted to the pursuit and capture of prey different from that of the predominately helicoid paryphantids and thus probably do not compete with the latter. Pupaeform streptaxids and helicoid paryphantids are both common in South Africa. In areas where the helicoid streptaxids are present, however, as in central and northern Africa, Central America, South America, and the mainland of Asia, the paryphantids are absent. This may indicate that the helicoid streptaxids have replaced the paryphantids whenever the two groups have come into competition. It is not known if there is a barrier preventing the spread of the helicoid streptaxids into South Africa, or whether the group is slowly extending its range and will eventually "eliminate" the paryphantids and occupy the entire African continent.

Helicoid streptaxids are found in southeastern Asia, but they are all small and do not equal the size of many African and American species. Possibly the carnivorous rathouisiid slugs of southeastern Asia utilize the food sources that the large helicoid streptaxids prey upon in other areas. A radiation of large helicoid streptaxids from another region could possibly compete successfully, but it is difficult to understand how early stages in the evolution of large streptaxids from small species could compete with the slugs. Possibly of significance is the fact that in areas where both paryphantids and rathouisiids are found (Lombok to the Bismarcks), no large paryphantids have been discovered. Northern Queensland may be an exception, and the ecological position of *Atopos australis* (Heynemann) and the large paryphantids needs investigation.

Except for the introduced *Gulella* (*Huttonella*) *bicolor* (Hutton), no streptaxids are known from the Indonesian area. Although common on the mainland, they do not seem to have crossed from Malaya

to Java and there is a puzzling absence of small carnivorous snails in the area from Java to Lombok. The cause of this distributional gap is unknown. Pupaeform and helicoid streptaxids have been found in the Celebes and Borneo (van Benthem Jutting, 1954), but these probably represent a recent invasion from the Philippines where streptaxids are common.

All the New Hebridean Paryphantidae belong to group "B." Examination of most of the named species resulted in my recognition of four broad categories based on shell sculpture and type of whorl increment. These groups are here considered genera. The type species are easily separable, but many species found near the geographical limits of distribution could be placed in more than one genus. Pending anatomical studies, it is probably better to maintain four large genera with several sections than to make each small species group a genus as Iredale did (1933, 1938). In the Malayan and Melanesian area, there are several conchological groups of species which have not been given generic names. One of these is so distinct that I have created a new subgenus, *Hebridelos*, for it.

A brief diagnosis of conchological characters is given for each of the genera and sections. All four genera of group "B" have been reported from the New Hebrides. The opportunity is taken to indicate the probable relationships of all the Pacific species and to classify the New Hebridean species.

#### Key to the New Hebridean Paryphantidae

1. Shell with definite surface sculpture . . . . . 2  
 Shell smooth, without definite surface sculpture.  
     *Macrocycloides annatonensis* (Pfeiffer)
2. Whorls rapidly increasing in width; body whorl at aperture as wide as spire. . . . . 3  
     (*Delos*)  
 Whorls slowly increasing in width; body whorl at aperture not as wide as spire. . . . . 5
3. Body whorl not sharply keeled . . . . . 4  
 Body whorl sharply keeled . . . . . *Delos gassiesi* (Pfeiffer)
4. Umbilicus shallow, wide at apex; whorls not laterally compressed. . . . .  
     *Delos rapida* (Pfeiffer)  
 Umbilicus deep, narrow at apex; whorls laterally compressed. . . . .  
     *Delos haasi*, new sp.
5. Umbilicus less than a fourth of the diameter in width . . . . . 6  
 Umbilicus more than half of the diameter in width.  
     *Ouagapia santoensis*, new sp.
6. Shell 10 mm. in diameter, with apertural tooth, weak transverse sculpture. . . . .  
     *Rhytida aulacospira* (Pfeiffer)  
 Shell more than 15 mm. in diameter, no apertural tooth, strong transverse sculpture. . . . . *Rhytida inaequalis* (Pfeiffer)

Genus **DELOS** Hutton, 1904

(= **Elaea** Hutton, 1883, not Ziegler, 1833, and **Rhenea** Hutton, 1893, not Saalmuller, 1884)

Paryphantids with whorls rapidly increasing in size, spire flat, depressed or only slightly elevated. Color pattern of reddish streaks or blotches. Surface sculpture of weak to strong spiral striae, growth lines and longitudinal striae never prominent.

*Type species*.—*Zonites coresia* Gray.

*Remarks*.—On the basis of the several types of shell sculpture observed in *Delos*, three subgenera and several sections are here tentatively recognized:

Subgenus *Delos* (sens. str.). Sculpture of very few short wavy spiral lines; much of the surface smooth.

Section *Delos* (sens. str.). New Zealand species. Umbilicus wide, coloration light. *Delouagapia* Powell, 1952, is probably a synonym.

Section *Prolesophanta* Iredale, 1933. Tasmanian species with a narrow umbilicus. *Tasmadelos* Iredale, 1933, is a synonym.

Subgenus *Saladelos* Iredale, 1933. East Australian species with narrow or wide umbilicus.

Subgenus *Hebridelos*, new subgenus. Species from the New Hebrides, Rotuma, and the Caroline Islands with prominent anastomosing spiral striae and dark red zigzag markings.

Subgenus **HEBRIDELOS**, new subgenus

Shell discoidal, spire flat or depressed. Whorls  $3\frac{3}{8}$  to  $4\frac{5}{8}$ , rapidly increasing in size. Umbilicus widely open, either shallow or deep, contained four to five times in the diameter. Body whorl rounded or keeled. Shell with thick epidermal layer. Color dark or light greenish-horn with red blotches or zigzag streaks. Sculpture of anastomosing spiral striae crossed by a few irregular growth lines. Aperture ovate to compressedly lunate, rarely deflected. Lip thin, simple. Diameter 5–12 mm., height 2–4 mm.

*Type species*.—*Helix rapida* Pfeiffer.

*Remarks*.—The color pattern and distribution (fig. 28) overlap *Ouagapia*, but the rapidly increasing whorls, narrow umbilicus, and spiral striae relate *Hebridelos* to *Delos*. Kondo (1943) investigated the anatomy of *D. (H.) oualanensis* (Pease) and two species of *Ouagapia*. The former differed in having a true verge. The drawings of Murdoch (1900) are incomplete, but it is probable that the genital anatomy of *Delos coresia* (Gray) is very similar to that of *D. oualanensis*.

The three New Hebridean species, *D. rapida* (Pfeiffer), *D. gassiesi* (Pfeiffer), and *D. haasi*, new sp.; *D. gardineri* Smith, 1897, from



Rotuma; and *D. oualanensis* (Pease) from the Caroline Islands are the only species in the subgenus *Hebridelos*. Previous accounts of *D. rapida* and *D. gassiesi* have been unsatisfactory, and for convenience they, as well as *D. haasi*, new sp., are here described.

**Delos (*Hebridelos*) *rapida* (Pfeiffer). Plate 11, figs. 1-3.**

*Helix rapida* Pfeiffer, 1853, Zeitschr. f. Malak., 1853: 54-55—New Zealand (error) (March); Pfeiffer, 1853, Conch. Icon., *Helix*, pl. 158, fig. 1038—New Zealand (error) (May); Pfeiffer, 1853, Proc. Zool. Soc. London, 1853: 58-59—New Zealand and Solomon Islands (error) (July 25); Cox, 1868, Monog. Austr. Land Shells, pp. 19-20, pl. 3, fig. 9, a, b—Cape York, Queensland and New Hebrides.

*Helix rapida* var. *beta* Pfeiffer, 1853, Zeitschr. f. Malak., 1853: 55—Solomon Islands.

?*Helix* (*Discus*) *rapida* Pfeiffer, Cox, 1868, Exchange List, p. 43, no. 92—Erromanga.

*Elaea rapida* (Pfeiffer), Tryon, 1885, Man. Conch., (2), 1: 129, pl. 26, fig. 13—New Zealand, Solomon Islands (errors); Hedley, 1890, Proc. Roy. Soc. Queensland, 6, (2), p. 100—New Hebrides.

*Rhenea rapida* (Pfeiffer), Sykes, 1903, Proc. Malac. Soc. London, 5: 196—Port Vila, Vate (J. J. Walker).

*Range*.—Vate, Erromanga(?).

*Material*.—New Hebrides (AMNH 55455, AMNH 65958, Marsh 6648, UMMZ 135627, ex Walker, Ponsonby); Vate Island (UMMZ 135626, ex Walker, Eaton; CM 62.5806, ex Hartman, Layard; MCZ, ex Putzeys); Vila, Vate (Miller 593 and USNM 598359, ex Miller); unknown locality (UMMZ 127597, ex Walker, Ponsonby). Photograph of syntype (BM).

Shell small, subdiscoidal, spire flat or slightly depressed. Whorls  $3\frac{3}{8}$  to  $3\frac{3}{4}$  (average  $3\frac{11}{16}$ ), rapidly increasing in size. Umbilicus shallow, wide at apex, contained about  $4\frac{1}{4}$  times in diameter. Body whorl obtusely rounded, not keeled. Shell with a thin calcareous and thick epidermal layer. Color greenish-horn with numerous reddish blotches. Occasionally blotches form zigzag stripes on lower surface. Surface sculpture of anastomosing spiral striae crossed by growth lines, stronger above, weaker below periphery. Below the epidermal layer, a sculpture of minute, transverse, anastomosing striae. Aperture ovate, rarely deflected. Lip thin, simple. Diameter 7.5-8.7 mm. (average 8.1); height 2.6-3.5 mm. (average 3.2).

*Remarks*.—Photographs of a syntype (pl. 11, figs. 1-3) enabled satisfactory identification of *Helix rapida* Pfeiffer. Moellendorff (1903, p. 18) was unable to identify the species and Hedley and Suter had previously stated that *rapida* did not live in either Australia or New Zealand. The syntype is identical with specimens from near Vila, Vate, and the type locality is restricted to the southern New Heb-

rides. Further restriction is impossible until more specimens of *Delos* (*Hebridelos*) *haasi*, new sp., are known. The possibility exists that the Erromangan specimens of *Delos* reported by Cox (1868) belong to *D. (H.) haasi*. If this is true the type locality of *D. (H.) rapida* could be restricted to Vate; if *D. (H.) rapida* is found on Erromanga as well as Vate, then Erromanga should be selected as type locality.

There is some variation in color pattern. Many specimens have the reddish blotches scattered, as in the syntype; others have the blotches organized into transverse stripes. Kondo (1943, p. 245) mentioned a dimorphic condition in *D. oualanensis*, where both a lightly sculptured and colored form and a heavily sculptured and darkly colored form were found together. The presence of both lightly colored and darkly colored specimens of *D. (H.) rapida* may indicate that a similar dimorphism exists in that species. *Delos (H.) rapida* has a wider, shallower umbilicus and fewer whorls than *D. (H.) haasi*, and it lacks the sharp keel which is characteristic of *D. (H.) gassiesi*.

***Delos (Hebridelos) gassiesi* (Pfeiffer). Plate 11, figs. 4, 6.**

*Helix gassiesi* Pfeiffer, 1861, Proc. Zool. Soc. London, 1861: 21—Erromanga (Turner); Pfeiffer, 1861, Malak. Blätt., 7: 234—Erromanga (Turner).

*Helix (Videna) gassiesi* Pfeiffer, Cox, 1868, Exchange List, p. 40, no. 45.

*Trochomorpha (Videna) gassiesi* (Pfeiffer), Clessin, 1881, Nomen. Helic. viv., p. 85, no. 1302—Erromanga.

*Range*.—Erromanga.

*Material*.—Erromanga (USNM, ex Calvert, Chamberlain); New Hebrides (AMNH 59127, ex Haines); photograph of holotype (BM).

Shell small, subdiscoidal, spire distinctly depressed below the body whorl. Whorls 4-4½, rapidly increasing in size. Umbilicus shallow, contained four times in diameter. Body whorl keeled, periphery at center of whorl. Keel slightly elevated, carina-like. Color pale horn, with transverse streaks of red. Sculpture of anastomosing spiral striae, stronger above the keel, weaker below. Subepidermal sculpture as in *D. (H.) rapida*. Aperture heart-shaped, laterally compressed. Lip thin, simple. Diameter 7.5-10.1 mm., height 2.7-3.8 mm.

*Remarks*.—The shallow umbilicus and size ally *Delos (Hebridelos) gassiesi* to *D. (H.) rapida*. The prominent keel probably misled Cox and Clessin, who placed *D. gassiesi* in the zonitid genus *Trochomorpha*. The specimens from the American Museum had the color pattern faded, but otherwise corresponded well to the type photographs. The single example from the U. S. National Museum was in a lot of *Gonatoraphe fornicata* (Pfeiffer). It is 10.1 mm. in diameter and 3.8 mm. high, and has 4½ whorls.

**Delos (Hebridelos) haasi**, new species. Plate 16, figs. 5-7.

A species of the subgenus *Hebridelos* distinguished from *D. (H.) rapida* (Pfeiffer) by its deeper, narrower umbilicus, weaker spiral sculpture, and laterally compressed whorls; from *D. (H.) gassiesi* (Pfeiffer) it is separated by its deeper, narrower umbilicus, weaker sculpture, and rounded (not keeled) body whorl.

Shell small, subdiscoidal, spire flat, not depressed. Whorls  $3\frac{7}{8}$  (paratypes  $4\frac{1}{4}$  to  $4\frac{5}{8}$ , average  $4\frac{3}{8}$ ), rapidly increasing in size. Umbilicus deep, very narrow at apex, contained about five times in the diameter. Body whorl rounded, slightly compressed laterally. Color greenish-horn with transverse zigzag red markings. Surface sculpture of a few weak anastomosing spiral striae. Subepidermal sculpture as in *D. (H.) rapida*. Aperture ovate, compressed laterally. Lip thin, simple. Diameter 7.5 mm. (paratypes 9.3-10.1 mm., average 9.6 mm.), height 3.0 mm. (paratypes 3.8-4.4 mm., average 4.1 mm.).

*Type*.—Dominion Museum, Wellington, New Zealand, no. M.F. 11263. Collected at 200 feet in forest on the island of Aneiteum, New Hebrides, by W. H. Dawbin, on October 22, 1954.

*Paratypes*.—UMMZ 127596 and CNHM 72440 with the locality "New Hebrides" from the Bryant Walker, John Ponsonby, and Andrew Garrett collections.

*Remarks*.—The Aneiteum holotype is much smaller than the paratypes, but the differences probably only reflect age or local environmental conditions. The specimens that Cox (1868) listed as *D. rapida* may actually have been *D. haasi*.

Great pleasure is taken in dedicating this species to my friend and mentor, Dr. Fritz Haas of Chicago Natural History Museum.

**Genus MACROCYCLOIDES** von Martens, 1869

Paryphantids with whorls gradually increasing in size, rounded, and with impressed sutures. Spire slightly elevated. Surface smooth with a few wide, low, growth lines, or widely spaced striae as in *Retinella*. Never with prominent spiral sculpture. Color hyaline or light horn with only traces of reddish flammulations. Aperture oblique, but not deflected.

*Type species*.—*Helix arthurii* Pfeiffer.

*Remarks*.—Species referable to *Macrocycloides* are found in Borneo (*arthurii* Pfeiffer), Amboina (*microcystis* Boettger), Saparua (*saparua* Boettger), Haruku (*sericina* Boettger), Ceram (*quadrispira* von Martens), New Guinea (*kaparensis* Smith), and the New Hebrides (*annatonensis* Pfeiffer) (fig. 27). Other species with flat spires, from Buru (*lutea* von Martens, *euglypta* von Martens) and the Solomon Islands (*veronica* Pfeiffer), do not seem separable. *Zonites hamelianus* Crosse and *Helix subnitens* Gassies, which Franc (1957, pp. 174-175)

placed in *Macrocyloides* are much smaller than any of the other species and are brown in color. It is very probable that they are ariophantids, not paryphantids. The "finement striée spiralement" of *subnitens* definitely removes it from the Paryphantidae, but without examination of specimens no suggestions can be made as to its systematic position.

The general appearance of the listed species is the same, but *Macrocyloides* may be polyphyletic. No species have been dissected and very few specimens are known. Without anatomical studies and abundant conchological material, recognition of more supraspecific categories is unwarranted.

Only a single species, *M. annatonensis* (Pfeiffer), is known from the New Hebrides.

**Macrocyloides annatonensis** (Pfeiffer). Plate 10, figs. 15–17.

*Helix annatonensis* Pfeiffer, 1854, Conch. Icon., *Helix*, pl. 200, fig. 1409—Aneiteum (MacGillivray); Pfeiffer, 1855, Proc. Zool. Soc. London, 1854: 288; Kobelt, 1897, Conch. Cab., I, 12, (4), pp. 552–553, pl. 166, figs. 14–15.

*Helix (Hyalinia) annatonensis* Pfeiffer, Cox, 1868, Exchange List, p. 38, no. 4—Aneiteum.

*Hyalinia (Polita) annatonensis* (Pfeiffer), Tryon, 1886, Man. Conch., (2), 2: 169, pl. 52, fig. 100.

*Rhytida (Macrocyloides) annatonensis* (Pfeiffer), Moellendorff, 1903, Conch. Cab., I, 12, (B), p. 48, pl. 9, fig. 7.

*Range*.—Aneiteum.

*Material*.—Aneiteum (CNHM 37019, ex Webb, Gude, Stevens); photographs of syntype (BM).

*Remarks*.—The size (9–10 mm. in diameter), pale coloration, very deep and wide umbilicus, and lack of spiral sculpture suffice to separate this species from the other New Hebridean paryphantids. The shell of *M. annatonensis* is superficially similar to some Asiatic and Malayan Helicarionidae, but the smooth surface and "greasy-white" color is characteristic of the carnivorous taxa. The only New Hebridean shell which is at all similar is the minute *Orpiella retardata* (Cox), which is 5 mm. in diameter and has a much smaller umbilicus. The single specimen of *M. annatonensis* that I saw, CNHM 37019, is 9.3 mm. in diameter, 4.6 mm. high, has 5 whorls, and the umbilicus is contained 3.1 times in the diameter.

Genus **RHYTIDA** Albers, 1860

Medium to large paryphantids with regularly coiled whorls, impressed sutures, and a deep, widely open umbilicus. Body whorl rounded or keeled. Sculpture of

prominent transverse ribs, reduced or absent in a few species. Spiral striae are prominent in some species, absent in others. Spire flat or elevated. Aperture large, lunate, not as oblique as in *Macrocyloides*.

*Type species*.—*Helix greenwoodi* Gray.

*Remarks*.—The species included in *Rhytida* can be divided into several conchological sections. Apparently there is a north-south gradation in sculpture which may prove of evolutionary importance when the genus has been thoroughly studied. New Zealand and Tasmanian species have very prominent transverse sculpture which usually is continued on the base of the shell; Australian and New Caledonian species have the sculpture weakened or absent on the base; and the species from the northern parts of Queensland have almost completely lost the transverse sculpture. On the basis of sculpture and distribution it is possible to recognize two subgenera and several sections. The following classification is suggested:

Subgenus *Rhytida* (sens. str.). Transverse ribs strongly developed on spire and body whorl or secondarily lost.

Section *Rhytida* (sens. str.). New Zealand species with transverse ribs on spire, sculpture becoming rugose to pitted on body whorl and base.

Section *Tasmaphena* Iredale, 1933. Tasmanian shells with transverse ribs on spire, body whorl and base.

Section *Strangesta* Iredale, 1933. East Australian species with transverse ribs on spire and body whorl above periphery. Base and body whorl below periphery smooth or with a few weak spiral striae. Probably *Montidelos* Iredale (1943a, p. 68) is synonymous.

Section *Murphitella* Iredale, 1933. Species from northern Queensland in which the transverse sculpture is lost and a very fine series of spiral lines has been developed. *Namoitena* Iredale, 1933, is a synonym.

Subgenus *Ptychorhytida* Moellendorff, 1903. A sculpture of widely spaced spiral lines has been developed in addition to the transverse ribs.

Section *Ptychorhytida* (sens. str.). New Caledonian shells with the transverse ribs well developed.

Section *Echotruda* Iredale, 1933. Australian species with the transverse sculpture greatly reduced.

Two species belonging to the subgenus *Ptychorhytida*, *aulacospira* Pfeiffer and *inaequalis* Pfeiffer, have been reported from the New Hebrides. Both are common in New Caledonia and probably the New Hebridean records are erroneous, since they originated from the Cuming collection. The two species are listed below but are not here accepted as being part of the New Hebridean fauna.

**Rhytida (Ptychorhytida) aulacospira** (Pfeiffer). Plate 10, figs. 10–12.

*Helix aulacospira* Pfeiffer, 1846, Proc. Zool. Soc. London, 1846: 37—no locality; Pfeiffer, 1853, Conch. Icon., *Helix*, pl. 150, fig. 975—New Hebrides (Cuming collection); Pfeiffer, 1854, Conch. Cab., I, 12, (3), p. 491, pl. 160, figs. 24–26.

*Helix multisulcata* Gassies, 1857, Jour. de Conchy., 6: 272–273, pl. 9, fig. 3—New Caledonia; Gassies, 1863, Faune Conchy. Nouv. Caledonie, I, p. 118, pl. 1, figs. 5–6.

*Rhytida multisulcata* (Gassies), Tryon, 1885, Man. Conch., (2), 1: 118, pl. 23, figs. 40–42.

*Patula (Punctum) aulacospira* (Pfeiffer), Tryon, 1887, Man. Conch., (2), 3: 35, pl. 7, fig. 86.

*Rhytida (Ptychorhytida) multisulcata* (Gassies), Moellendorff, 1903, Conch. Cab., I, 12, (B), pp. 71–72, pl. 12, figs. 6–8.

*Rhytida (Ouagapia) aulacospira* (Pfeiffer), Moellendorff, 1904, Conch. Cab., I, 12, (B), pp. 81–82, pl. 13, figs. 6–8.

*Ouagapia (Ptychorhytida) aulacospira* (Pfeiffer), Franc, 1957, Mem. Mus. Nat. Hist. Nat., n.s., Zool., 13: 173, pl. 22, fig. 230.

*Range*.—New Caledonia and Loyalty Islands.

*Material*.—New Hebrides (ANSP 23685, ex Wilschach); New Caledonia (several lots in UMMZ, ANSP, CNHM). Photograph of syntype (BM).

*Remarks*.—Sykes (1895, p. 72) united *aulacospira* and *multisulcata* after examining the types in the British Museum (Natural History). *R. aulacospira* is a common New Caledonian shell and the New Hebridean record from the Cuming collection is probably incorrect. The ANSP lot was identified as "*Delos rapida*," a New Hebridean shell (see p. 153), and may have been mislabeled. Photographs of the syntype of *aulacospira* are reproduced here (pl. 10, figs. 10–12) for convenient reference.

**Rhytida (Ptychorhytida) inaequalis** (Pfeiffer)

*Helix inaequalis* Pfeiffer, 1854, Conch. Icon., *Helix*, pl. 198, fig. 1394—Isle of Pines (MacGillivray); Pfeiffer, 1854, Proc. Zool. Soc. London, 1854: 286; Gassies, 1863, Faune Conchy. Nouv. Caledonie, I, p. 32, pl. 1, fig. 17.

*Helix fischeri* Gassies, 1857, Jour. de Conchy., 6: 271, pl. 9, figs. 1, 2.

*Rhytida (Ptychorhytida) inaequalis* (Pfeiffer), Moellendorff, 1904, Conch. Cab., I, 12, (B), pp. 75–76, pl. 12, figs. 17–19.

*Ouagapia (Ouagapia) inaequalis* (Pfeiffer), Franc, 1957, Mem. Mus. Nat. Hist. Nat., n.s., Zool., 13: 169, pl. 21, fig. 225.

*Range*.—New Caledonia.

*Material*.—New Hebrides (ANSP 1909, ex A. D. Brown; MCZ 10990, ex Anthony, Cuming; CM 62.14564, ex Hartman); New Caledonia (UMMZ 11040, ex Stearns; UMMZ 135598, ex Walker, Wetherby; UMMZ 135599, ex Walker, Ponsonby, Garrett, Layard; UMMZ 135600, ex Walker, Ponsonby, Layard).

*Remarks*.—Layard, in his letters to Hartman, did not mention *R. inaequalis* as a New Hebridean shell, although the Hartman collection contains many New Caledonian specimens received from Layard. The source of the New Hebridean locality probably was the Cuming collection, the localities of which are notoriously inaccurate. *R. inaequalis* is characterized by its size, strong spiral and transverse sculpture, and lack of an apertural tooth.

#### Genus **OUAGAPIA** Crosse, 1894

Small to large paryphantids with a deep, wide umbilicus. Whorls increasing regularly in size, sutures impressed and channeled. Color horn with reddish maculations. Sculpture varies.

*Type species*.—*Helix raynali* Gassies.

*Remarks*.—There are three species groups included in *Ouagapia*. Diverse in size and sculpture, their common color pattern and island distribution (fig. 27) have resulted in their being united. Rather than add more names to the overburdened taxonomy, the species are here retained in the same genus.

The genotype, *O. raynali*, is very large, with a shell sculpture of prominent but very fine, close-set spiral lines. The same sculpture is found on the base of *Rhytida* (*Murphitella*) *franklandensis* (Forbes) (UMMZ 135582, ex Walker, Thompson, Brazier, MacGillivray from Frankland Island, Queensland). The color patterns of *raynali* and *franklandensis* are quite different, but since neither has been dissected their relationship is uncertain.

*O. villandrei* (Gassies) from the Solomon Islands (see Clapp, 1923) is very similar to *raynali* in size, color pattern, and size of umbilicus. *O. villandrei* differs in having the base of the shell with only a few weak, irregular spiral striae and the upper portion with strong transverse ribs as in the third group.

The third group consists of *O. gradata* (Gould) from Samoa and Tonga (see Kondo, 1948); *O. ratusukuni* (Cooke) from the Fijis; *O. opaoana* (Gassies), *O. lamberti* (Gassies), and *O. rufotincta* (Gassies) from New Caledonia; *O. santoensis*, new sp., from the New Hebrides; and, less certainly, *O. radicalis* (Mousson) and *O. vicaria* (Mousson) from Tonga. All have a deep, very wide umbilicus; trans-

verse sculpture above the periphery; and spiral lines below the periphery of the body whorl. "*Rhytida*" *bednalli* Ponsonby, 1907, from New Guinea, "*Endodonta*" *acuticarinata* Thiele, 1928, from New Britain, and "*Charopa*" *delectans* Smith, 1898, from New Guinea also seem to belong to this series of *Ouagapia* (see Solem, in press-B).

Only *O. gradata* and *O. ratusukuni* have been dissected (Kondo, 1943). Until the large New Caledonian and Solomon Island *Ouagapia* have been dissected, taxonomic recognition of the three groups outlined above would be unwise. Probably the genus *Ouagapia*, as now constituted, is polyphyletic. *O. santoensis*, new species, was collected from ground detritus in the Sarakata River Valley on Espiritu Santo. Only dead shells were found.

***Ouagapia santoensis*, new species. Plate 28, figs. 6-8.**

?*Nanina* (*Endodonta*) *acetabulum* Mabile (not Pease), 1895, Bull. Soc. d'Hist. Nat. d'Autun, 8: 409—New Hebrides (François).

A species of *Ouagapia* related to *O. opoana* (Gassies) and *O. gradata* (Gould) but distinguished from them by having a wider, shallower umbilicus, the base of the shell more sharply keeled, the spire and body whorl narrower, and the coloration lighter.

Shell small, flat, discoidal. Spire slightly elevated or flat, sutures impressed and channeled. Whorls  $3\frac{3}{4}$  to 4, gradually increasing in size. Umbilicus widely open, more than one half of the diameter in size. Base of shell distinctly keeled around the umbilicus. Sculpture of prominent, close-set, transverse ribs on the spire and above the periphery of the body whorl. Below the periphery and in the umbilical region a sculpture of a few growth lines and weak, widely spaced spiral striae. A few fine, close-set spiral striae on the spire. Color light horn, with a few irregular transverse reddish maculations. Aperture large, lunate, sharply angled below. Lip thin, simple. Diameter 5.5-5.8 mm., height 2.4-2.8 mm.

*Type*.—University of Michigan Museum of Zoology no. 188435. Collected from stream drift in the Sarakata River Valley, Espiritu Santo, New Hebrides (ML 95), by Robert E. Kuntz in May and June, 1944.

*Paratypes*.—On Espiritu Santo, specimens were collected from ML 33 and ML 95 (type locality). Paratopotypes are UMMZ 188436 and CNHM 73061. One paratype is UMMZ 188437.

*Remarks*.—Mabile's record for the Polynesian endodontid *Nesodiscus acetabulum* was probably based on *O. santoensis*. In size, shape, and color the two species are very similar, despite their very different taxonomic positions. Similar convergence probably caused I. Rensch (1937) to place the Bismarck *Ouagapia acuticarinata* (Thiele) in *Nesodiscus*.



*O. santoensis* has a wider umbilicus than that of any other species except *O. ratusukuni* Cooke (UMMZ 164673), which is larger and flatter and lacks the color flammulations of the New Hebridean shell.

### Superorder **BASOMMATOPHORA** Schmidt, 1855

Snails bearing eyes at base of a pair of contractile, but not invaginable tentacles. Animals hermaphroditic, with separate genital openings, the male more anterior. Shell external, variously modified. Respiration through lung, gills, and/or epithelium. Except for the tidal, estuarine, and terrestrial Ellobiidae, marine Patelliformia, and estuarine Amphibolidae, the Basommatophora are fresh-water inhabitants.

Three families, the Siphonariidae, Ellobiidae, and Planorbidae, are found in the New Hebrides. The Siphonariidae belong to the littoral fauna and will be considered with the other marine taxa. The Ellobiidae contain tidal, supratidal, and estuarine species which tend to form local colonies showing a wide range of morphologic variation. Similar situations complicate the study of the Thiariidae and *Neritina* (sens. lat.) and the Ellobiidae will be considered with the latter. Both the Siphonariidae and Ellobiidae belong to the more primitive "Archaeopulmonata" (Morton, 1955, p. 163), perhaps more often called, respectively, parts of the "Thalassophila" and "Actophila" (Hubendick, 1945, p. 164). The Planorbidae, together with the Lymnaeidae, Ancyliidae, and Physidae, form the Hygrophila (Thiele, 1931), "higher limnic Basommatophora" (Hubendick, 1945), or "Branchiopulmonata" (Morton, 1955).

Comprehensive surveys of the relationships and phylogeny of the Basommatophora can be found in Hubendick (1945), Graham (1949), and Morton (1955).

### Family **PLANORBIDAE**

Shell basically sinistral, flat, discoidal, lens-shaped, ovate, or turreted, but pseudodextral in many taxa. Foot small, broad; tentacles slender. Most species with a secondary gill (pseudobranch) below pulmonary orifice on the left side. Radula with normally bicuspid central tooth, tricuspid laterals, and serrate marginals (Mandahl-Barth, 1954, p. 72).

Because certain planorbid snails are vectors of an important human parasitic disease, schistosomiasis or bilharzia, much attention has been focused on the Planorbidae in recent years. Most reports have been restricted to the few species of immediate medical importance, but the studies of Hubendick (1948, 1955) and Mandahl-Barth (1954) supplement the systematic conclusions presented in the uncompleted

monograph by F. C. Baker (1945), which was published posthumously. The classification below follows Hubendick (1955).

Two genera, *Gyraulus* and *Physastra*, are found in the New Hebrides. *Gyraulus* is probably world-wide in distribution; *Physastra* is restricted to the Indo-Australian region. The single species of each genus is also found in New Caledonia.

#### Subfamily PLANORBINAE

Genus **PHYASTRA** Tapparone-Canefri, 1883

*Type species.*—*Physastra vestita* Tapparone-Canefri.

*Remarks.*—Prior to 1948, the Indo-Melanesian physoid snails were grouped with the African carriers of bilharzia as *Bulinus* (sens. str.). Hubendick (1948) demonstrated that there are two types of “*Physa*”-like planorbs. One, the Afro-Australian *Bulinus*, has the male copulatory organ with a pseudopenis (Hubendick, 1948, p. 25, fig. 93). It is placed in a subfamily, the Bulininae. The Planorbiniae contain species with a true penis and seem to be more primitive than the Bulininae.

Three genera of physoid planorbinine shells are recognized; *Physastra*, in which the penis has a horny terminal stylet and a lateral penis pore; *Amerianna*, which has no stylet and a terminal penis pore; and *Miratesta*, which has a lateral pore but no stylet. The distribution and probable synonyms of the genera are given by Hubendick (1948, pp. 57–59).

Franc (1957, pp. 83–88) recognized twelve “species” of *Physastra* from New Caledonia. Material in the University of Michigan Museum of Zoology suggests that most of the “species” should be united into one taxon. Layard expressed a similar opinion in a letter to Hartman (March, 1890), since he had often observed different “species” of *Physastra* in copulation. The earliest name available for the New Caledonian *Physastra* is *nasuta* Morelet, 1856. Union of the named forms into one species is premature, but probably will be eventually accomplished. Several Fijian specimens (*sinuata* Gould, 1852) in the material studied do not differ from the New Hebridean and New Caledonian shells. If the possible relationship of the Tongan population (*tongana* Quoy and Gaimard, 1832) is also considered, obviously no decision on the specific status or names of the Melanesian *Physastra* can be reached at this time. Until the majority of the named entities can be critically examined, both as to anatomy and

shell structure, any name applied to the complex must be only provisional.

Hubendick (1948, p. 16, figs. 50–53, 58, pl. 1, fig. 4) partially figured the anatomy of *Physastra doliolum* (Gassies) from Kone, New Caledonia. I dissected several specimens from Espiritu Santo. No differences of any significance were found. Proportional size and details of the penial region were identical. Without any doubt the New Hebridean populations and New Caledonian *doliolum* belong to the same species. Unfortunately, no other Melanesian *Physastra* has been dissected.

Little would be accomplished by uniting the New Hebridean population to *P. doliolum* only, and it is premature to synonymize all of the New Caledonian species. For convenience, Ancey's name, *Physa layardi*, is used for the New Hebridean *Physastra* until such time as the remaining Melanesian *Physastra* can be studied.

### **Physastra layardi** (Ancey). Plate 25, figs. 10–14.

*Physa sinuata* Mabille (not Gould, 1852), 1895, Bull. Soc. d'Hist. Nat. d'Autun 8: 409—New Hebrides (François).

*Physa layardi* Ancey, 1905, Nautilus, 19, (4), p. 44—Vate (Glisson).

*Isidora caledonica* Boettger (not Morelet, 1856), 1916, Abhl. Senck. Naturf. Gesell., 36, (3), p. 296—Aniwa.

*Physa* cf. *obtusa* J. R. Baker, 1929, Man and animals in the New Hebrides, p. 148—Steaming Hill Lake, Gaua, Banks Group.

*Range*.—Espiritu Santo, Gaua, Vate, Aniwa, Tanna, Aneiteum, Aore and Futuna.

*Material*.—ML 60, ML 61a, ML 61b, ML 62, ML 65, ML 68, ML 78, ML 80, ML 82a, ML 82b, ML 85a, ML 85b, ML 91, ML 93; Vate (CM, ex Hartman, Layard, type lot material; DMNZ, W. H. Dawbin!, at 800 feet elevation); Aniwa (CNHM 35109, ex Boettger); Tanna (MCZ, ex BPBM 81642); Anelgauhat, Aneiteum (DMNZ, M. Laird!); Aneiteum (DMNZ, M. Laird!); Aore (DMNZ, M. Laird!); Imatangi Village, Futuna (DMNZ, M. Laird!).

*Remarks*.—The juvenile specimens (type lot; CM) compare well with the original description of *P. layardi* (Ancey). On Espiritu Santo, adult shells were collected May 5, but only very young shells (5–6 mm.) in late May and June. Slightly larger specimens (7–10 mm.) were found in late July. Most of the material came from a semi-permanent pond near Brigstock Point. Kuntz recorded in his field notes that the animals were infected with small stylet cercariae. Locality ML 68 was in a flowing creek; otherwise all specimens were from still water.

The conchological variation found within a single population of *P. layardi* is exceptionally large (pl. 25). Such plasticity of form is well documented in physoid Planorbidae and appears to be the norm rather than the exception (see Hedley, 1917; Mandahl-Barth, 1954, pp. 101–116). The largest specimen of *P. layardi* was 19.4 mm. high and 10 mm. in diameter, with  $6\frac{1}{4}$  whorls. Most individuals collected in July (ML 85) were the size (10 mm. high) and whorl count (5 whorls) of the cotypes from Vate (CM). Specimens from the other islands were well within the range of variation found in the Espiritu Santo population. I have assumed that the Gaua population does not differ significantly.

Several individuals from ML 65 were dissected. The jaw, radula, and distal male genitalia were compared to the figures in Hubendick (1948). No differences were found between the Espiritu Santo animals and *Physastra doliolum* (Gassies), which Hubendick studied. The anatomy is not refigured.

#### Genus **GYRAULUS** Charpentier, 1837

*Type species*.—*Planorbis hispidus* Draparnaud (= *albus* Müller).

*Remarks*.—*Gyraulus*-like snails are found in fresh water nearly everywhere. Little is known of their anatomy, and the generic position of most of the Indo-Pacific species is very poorly understood. The New Hebridean *G. montrouzieri* (Gassies) has not been dissected. The shell is very similar to that of the Indonesian *G. convexiusculus* (Hutton), which is a typical *Gyraulus* (F. C. Baker, 1945, pp. 67–70).

#### **Gyraulus (Gyraulus) montrouzieri** (Gassies). Plate 33, figs. 10–12.

*Planorbis montrouzieri* Gassies, 1863, Faune Conchy. Nouv. Caledonie, I, p. 283, pl. 7, fig. 17—Kanala, New Caledonia; Bavay, 1908, Nova Guinea, Zool., 5: 289—Lac Sentani, Dutch New Guinea.

*Planorbis (Spirodiscus) montrouzieri* Gassies, Crosse, 1894, Jour. de Conchy., 42: 334–335.

*Planorbis (Gyraulus) montrouzieri* Gassies, Germain, 1923, Rec. Indian Mus., 21, (3), pp. 147–148, pl. 2, figs. 7–9.

*Gyraulus montrouzieri* (Gassies), F. C. Baker, 1945, Molluscan family Planorbidae, p. 71; Franc, 1957, Mem. Mus. hist. nat., n.s., Zool., 13: 90, pl. 9, fig. 122.

*Range*.—Espiritu Santo, New Caledonia, possibly New Guinea.

*Material*.—ML 62, ML 85a, ML 85b, ML 82a; Kanala, New Caledonia (ANSP 71178, ex Vanatta, topotypes); New Caledonia (ANSP

21694, ex Marie; UMMZ 16116, ex Stearns; UMMZ 86793, ex Walker, MacAndrews).

*Remarks.*—Topotypes of *G. montrouzieri* (ANSP 71178) were more sharply carinated than most of the New Hebridean shells. The figures in Germain (loc. cit.) and the other New Caledonian specimens, however, all closely approximated the Kuntz series. There are several species of New Caledonian "*Planorbis*" (see Franc, 1957, pp. 89–91, figs. 121–123).

Related extralimital species include all the *Glyptaniscus* of Iredale (1943b, pp. 225–227) and Cotton (1943) and *G. convexiusculus* (Hutton). The Australian *Glyptaniscus* appear to be badly oversplit and the genus itself is probably only a section of *Gyraulus* (sens. str.). Australian material (UMMZ) is intermediate between *montrouzieri* and *convexiusculus* in that the umbilicus is moderately excavated and the apical whorls are deeply sunken; in *montrouzieri* the base is rather deeply excavated and the apical whorls are only slightly sunken; and in *convexiusculus* the base is nearly flat and the apical whorls are sunken well below the level of the spire. *G. montrouzieri* differs from both *Glyptaniscus* and *convexiusculus* in having a submedian rather than a median keel.

*G. convexiusculus* has an exceedingly wide range of variation, and long synonymy. Information on this species is summarized in the papers of van Benthem Jutting (1931), B. Rensch (1934), and Bequaert and Clench (1939). Definitely known from as far east as the Celebes and Buru, probably *Gyraulus elberti* Haas, 1912, from Lombok, and *Planorbis turbinellus* Tapparone-Canefri, 1883, from the Aru Islands, will be added to the synonymy of *G. convexiusculus*. The report of *montrouzieri* from New Guinea needs confirmation. It may only be a new record for *convexiusculus*.

Three of the New Hebridean series, ML 82a, ML 85a, and ML 85b, were collected in June and July from the quiet waters of a dammed

Table XI.—Measurements of *Gyraulus montrouzieri* (Gassies)

|                  | Greater diameter | Lesser diameter | Height | H/D  | Umbilicus | Whorls          |
|------------------|------------------|-----------------|--------|------|-----------|-----------------|
| ANSP 71178 . . . | 4.47             | 3.70            | 1.25   | 0.35 | 1.55      | 3 $\frac{3}{4}$ |
| (topotypes) . .  | 4.17             | 3.52            | 1.21   | 0.29 | 1.49      | 3 $\frac{5}{8}$ |
|                  | 4.00             | 3.22            | 1.12   | 0.28 | 1.29      | 3 $\frac{3}{8}$ |
| ML 62 . . . . .  | 5.93             | 4.78            | 2.05   | 0.35 | 2.17      | 4 $\frac{1}{4}$ |
|                  | 5.30             | 4.44            | 1.99   | 0.38 | 1.99      | 4               |
|                  | 4.73             | 3.82            | 1.54   | 0.34 | 1.59      | 3 $\frac{3}{4}$ |
|                  | 4.16             | 3.54            | 1.31   | 0.31 | 1.37      | 3 $\frac{1}{2}$ |
| ML 85 . . . . .  | 4.05             | 3.31            | 1.48   | 0.34 | 1.37      | 3 $\frac{5}{8}$ |
|                  | 3.76             | 3.08            | 1.42   | 0.38 | 1.14      | 3               |

creek and a fresh-water pool connected with the creek. The shells were appreciably smaller than those collected in May from a semi-permanent pond (ML 62) on the east side of Brigstock Lagoon. The differences were in whorl count and diameter, large specimens from the first three series having the same whorl count and diameter as small specimens from the fourth. Generally the larger specimens were more sharply keeled. Diameter is directly dependent on whorl count, and measurements of several shells are given in Table XI for comparative purposes. As in all Pacific *Gyraulus* there is much variation in the degree of carination.

### Subclass PROSOBRANCHIA Milne-Edwards, 1848

The recent prosobranch classification of Thiele (1929) has been accepted here without major changes, and diagnoses of the higher categories are not usually given below. An expanded classification, including the fossil mollusks, can be found in Wenz (1938-44).

Several prosobranch families—the Neritidae, Viviparidae, Ampullariidae, Valvatidae, Hydrobiidae, Micromelanidae, and Thiaridae—colonized the fresh-water habitat, while others—the Hydrocenidae, Helicinidae, Cyclophoracea, Truncatellidae, Pomatiasidae, Acmidae, and Assimineidae—have become land dwellers. The only truly fresh-water prosobranch known from the New Hebrides is the hydrobiid, *Fluviopupa brevior* (Ancey). Many “primary” fresh-water Neritidae and Thiaridae are found in other areas of the world, but none are known from the New Hebrides. All the Melanesian Thiaridae and Neritidae seem capable of passing salt water filter zones with relative ease and are very widely distributed. Of the land prosobranch families, the Helicinidae, Cyclophoracea, Truncatellidae, and Assimineidae are native to the New Hebrides.

## Order ARCHAEOGASTROPODA

### Superfamily NERITACEA

#### Family HELICINIDAE

Shell imperforate, strongly depressed to conic, with few whorls. Umbilical region covered by a prominent callus. Operculum with thin to moderately heavy calcareous layer, either concentric or paucispiral. Radula rhipidoglossate. Foot broad, undivided or tripartite. (Modified from Pilsbry, 1948, p. 1078.)

The most recent monograph of the Helicinidae (Wagner, 1907-11) is very inadequate. The illustrations are useless, no attention

has been paid to the work of previous authors, nomenclatural procedure is not followed, and errors in citation, fact, and localities are many. Fulton (1915) listed 137 species of Helicinidae which Wagner did not even mention. In recognizing the distinctness of the Antillean and Indo-Pacific helicinids, Wagner made a valuable contribution, but the numerous errors and omissions mar the otherwise favorable impression that his work merits.

Six new genera, and many subgenera, based entirely on shell and opercular characters, were established by Wagner. Unfortunately he did not designate type species, and over a span of two or three years he indiscriminately shifted species from genus to genus. H. B. Baker (1922), Thiele (1929), Pilsbry and Cooke (1934b), Iredale (1937a), and Wenz (1938-44, pp. 435-444) all tried to settle the nomenclatural status of Wagner's genera. Iredale (1937a, pp. 291-293) complicated the issue by accepting Wagner's "Formenkreise" as formally proposed sectional names. They were not intended as such, being simply "species groups" often designated by the trivial name of one of the included species (see Zilch, 1948).

A list of the available generic units of Pacific helicinids follows, giving type designations and geographic range:

**Waldemaria** A. J. Wagner, 1905

*Type species.*—*Helicina japonica* A. Adams, by subsequent designation of H. B. Baker (1922, p. 41).

*Range.*—Japan. This is a section of the North American *Hendersonia*.

**Sulfurina** Moellendorff, 1893

*Type species.*—*Helicina citrina* Grateloup.

*Range.*—Indonesia, the Philippines, Nicobar, Palau, and the Caroline Islands (see fig. 23).

**Sturanyella** Pilsbry and Cooke, 1934

*Type species.*—*Helicina plicatilis* Mousson.

*Range.*—Carolines, Solomons, Fiji, Tonga, Wallis, Samoa, Cook, and (?)Galapagos (see fig. 22).

*Remarks.*—*Sturanyella* is a new name for the group usually called *Sturanya* Wagner. The latter name was transferred to *Orobophana* (see below) by the type designation of H. B. Baker (1922).

**Gophorus** Fischer, 1885 (see Bartsch, 1918)

*Type species.*—*Helicina agglutinans* Sowerby.

*Range.*—Philippines and Indonesia (see fig. 23).

**Pleuropoma** Moellendorff, 1893

*Type species.*—*Helicina dichroa* Moellendorff.

*Range.*—Indo-Pacific Islands except Tuamotus, Marianas, and Marshalls (see fig. 22).

Synonyms of *Pleuropoma* are:

**Aphanoconia** Wagner, 1905

*Type species.*—*Helicina verecunda* Gould, by subsequent designation of Gude (1921, p. 366).

**Sphaeroconia** Wagner, 1905

*Type species.*—*Helicina verecunda* Gould, by subsequent designation of H. B. Baker (1922, p. 43).

**Orobophana** Wagner, 1905

*Type species.*—*Helicina uberta* Gould, by subsequent designation of H. B. Baker (1922, p. 43).

*Range.*—New Caledonia(?), Fiji, Tonga, Cook, Niue, Society, Tuamotus, Marquesas, and Hawaii (see fig. 23).

**Sturanya** Wagner, 1905

*Type species.*—*Helicina laciniosa* Mighels by subsequent designation of H. B. Baker (1922, p. 43).

*Remarks.*—Johnson (1949, p. 226) clearly showed that the *Helicina laciniosa* of authors (for example, Neal, 1934) is not the *laciniosa* of Mighels. The latter is equivalent to *Orobophana berniceia* Pilsbry and Cooke, which means that *Sturanya* becomes a subjective synonym of *Orobophana*, and no name of generic rank is available for the "zonata" group of *Pleuropoma* (see p. 177). No substitute name is proposed, since the generic value of the latter group is doubtful.

**Palaeohelicina** Wagner, 1905

*Type species.*—*Helicina moquiniana* Recluz, by subsequent designation of Thiele (1929, p. 87).

*Range.*—The Solomons, Bismarcks, New Guinea, and Palau Islands (see fig. 23).

**Ceratopoma** Moellendorff, 1893

*Type species.*—*Helicina caroli* Kobelt.

*Range.*—The Philippines, Indonesia, and Australia (see fig. 22).

*Remarks.*—Wagner considered *Ceratopoma* to be a subgenus of his later genus *Palaeohelicina*. *Ceratopoma* has priority, and if the two prove to be related, *Ceratopoma* must be used as the generic name.

The above list is primarily nomenclatural, since little is known about the Pacific Helicinidae. Bourne (1911), H. B. Baker (1922, 1925b, 1926), and van Benthem Jutting (1941) published papers on the anatomy of the Helicinidae. Very few Pacific species have been examined. Bourne (1911) dissected four *Pleuropoma*, one *Orobophana*, and a *Ceratopoma*. H. B. Baker (1922) studied the radulae of *Waldemaria* and *Pleuropoma verecunda* (Gould), and van Benthem Jutting (1941, p. 6) the radula of *Sulfurina cerinella* van Benthem Jutting. These papers and the brief note on Hawaiian helicinids by Pilsbry and Cooke (1909) form the total published knowledge of the Pacific Helicinidae.



*Orobophana* has a distinctive radula, but there are only minor differences between *Pleuropoma*, *Sturanya*, *Aphanoconia* and *Ceratopoma*. Animals of three New Hebridean species were available. I saw no extralimital specimens, and, other than radular mounts, did not study the anatomy. On the basis of radular structure, the New Hebridean species are here placed in *Pleuropoma*. The radula of the Helicinidae is extremely complex and difficult to interpret correctly (see H. B. Baker, 1922, p. 33). Since no comparative material was available and I have not previously worked with helicinid anatomy, the radulae are not figured at this time. The radulae of *Pleuropoma varians* (Sykes), *P. albescens* (Hartman), and *P. sublaevigata* (Pfeiffer) are extremely similar and apparently there are no major differences between them.

The land operculates are all dioecious and in many genera there is considerable sexual dimorphism. In the Neritidae, Hydrobiidae, Cyclophoracea, and Assimineidae the females are much larger than the males and the males have a prominent cephalic penis. In the Helicinidae there are no external sexual differences, and H. B. Baker's (1925b, pp. 274-275) attempt to determine sexual dimorphism yielded mainly negative results. It was not possible to undertake a study of sexual dimorphism in the present investigation.

Wagner (1907-11) and Bourne (1911, pp. 760-762) discussed the geographic distribution of the Helicinidae. The family is absent from Europe, Africa, most of Asia, New Zealand, Norfolk and the Lord Howe Islands, and much of Australia. Most helicinids are found in the Greater Antilles and the Indo-Polynesian region. There are only a few continental relatives, and very few species live outside the tropics.

Twelve species of Helicinidae have been described from the New Hebrides. Only six are here accepted as valid; three, *modesta* Pfeiffer, *zebriolata* Pfeiffer, and *subreticulata* Wagner, are probably based on erroneous locality data; and three, *bairdii* Reeve, *layardi* Hartman, and *novella* Mabile, are reduced to synonymy. Of the six recognized species, one, *Pleuropoma articulata* (Pfeiffer), is related to a widely distributed group, while the other five, *P. varians* (Sykes), *P. taeniata* (Quoy and Gaimard), *P. albescens* (Hartman), *P. sublaevigata* (Pfeiffer), and *P. rotella* (Sowerby), form a homogeneous series without discernible extralimital relatives. No preserved material of *P. articulata* was available, but subsequent study may place this species in a different genus from the others. There is no apparent relationship between the Solomon Island and New Hebridean Helicinidae, and

only a weak one between the New Hebridean and New Caledonian species.

Key to the New Hebridean Helicinidae

1. Body whorl with knife-edge carina; diameter more than 9 mm. . . . . 2  
 Body whorl rounded or angulated; if carinate, then diameter less than 6.5 mm. . . . . 3
2. Columellar margin with basal tooth; Vanikoro.  
*Pleuropoma taeniata* (Quoy and Gaimard)  
 Columellar margin without basal tooth; Santa Cruz Island. . . . . *P. varians* (Sykes)
3. Color pattern of spiral bands or unicolored. . . . . 4  
 Color pattern of alternating red and white radial flammulations.  
*P. articulata* (Pfeiffer)
4. Body whorl angulated; lip strongly reflected; weak columellar sinus. . . . . 5  
 Body whorl rounded; lip weakly reflected; strong columellar sinus.  
*P. sublaevigata* (Pfeiffer)
5. Shell larger, 9–11 mm.; Tanna. . . . . *P. rotella* (Sowerby)  
 Shell smaller, 6–8 mm.; Espiritu Santo. . . . . *P. albescens* (Hartman)

Genus **PLEUROPOMA** Moellendorff, 1893

In accordance with the determinations of H. B. Baker (1922), Pilsbry and Cooke (1934b), and Wenz (1938–44), *Aphanoconia* and its synonym *Sphaeroconia* are here considered congeneric. *P. articulata* would be placed in the *zonata* group, if the latter proves to be separable, while the other New Hebridean species form an isolated group of *Pleuropoma*. Anatomical studies may reveal that the New Hebridean species belong in a special section, but nomenclatural recognition is not warranted at this time.

**Pleuropoma varians** (Sykes). Plate 26, figs. 3, 4.

*Helicina varians* Sykes, 1903, Jour. of Malac., **10**, (2), p. 67—Santa Cruz Islands; Sykes, 1903, op. cit., **10**, (13), p. 78, pl. 6, figs. 5, 6.

*Range*.—Santa Cruz, Santa Cruz Islands.

*Material*.—Santa Cruz Island (UMMZ 72060, ex Walker, Ponsonby, Sykes, paratypes; MCZ 32609, ex W. M. Mann!).

*Remarks*.—*P. varians* superficially resembles the northern Melanesian *Palaeohelicina*, but it lacks the spiral striae of that genus and has the same embryonic spiral ridges, deciduous periostracal bands, and type of radula found in the New Hebridean *Pleuropoma*. Most of the 89 individuals that I examined were yellow with red supra-peripheral color band, but others were uniform yellow and a few had radiating reddish-brown color streaks. The variation in size and

Table XII.—Size Variation in New Hebridean *Pleuropoma*

| Species                                     | No. of specimens | Height |         |      | Diameter |          |      | H/D ratio |       |      | Whorls |
|---|------------------|--------|---------|------|----------|----------|------|-----------|-------|------|--------|
|   |                  | Mean   | Range   | S.D. | Mean     | Range    | S.D. | Mean      | Range | S.D. |        |
| <i>P. albescens</i> (Htm.) (ML 32).....     | 67               | 5.21   | 4.6-5.8 | 0.19 | 6.93     | 6.3-7.7  | 0.25 | 75.3      | 69-84 | 2.72 | 4½-4½  |
| <i>P. sublaevigata</i> (Pfr.) (ML 26f)..... | 24               | 5.21   | 4.8-6.1 | 0.28 | 7.20     | 6.5-7.5  | 0.26 | 72.1      | 68-82 | 2.80 | 4-4½   |
| <i>P. varians</i> (Sykes) (MCZ).....        | 59               | 6.15   | 5.6-6.8 | 0.29 | 10.2     | 9.1-11.6 | 0.56 | 60.5      | 52-68 | 3.00 | 4-4¾   |
| (UMMZ 72060, paratypes).....                | ..               | 6.8    |         |      | 11.4     |          |      | 60        |       |      | 4¼     |
| <i>P. articulata</i> (Pfr.)                 |                  | 6.3    |         |      | 10.4     |          |      | 61        |       |      | 4½     |
| Vate Island                                 |                  |        |         |      |          |          |      |           |       |      |        |
| (Miller 69) 1943.....                       | 10               | 3.45   | 3.2-3.7 | 0.12 | 5.0      | 4.8-5.4  | 0.20 | 68.6      | 64-74 | 2.00 | 3¾-4½  |
| (DMNZ) 1954.....                            | 14               | 2.82   | 2.6-3.1 | 0.12 | 4.3      | 3.9-4.5  | 0.19 | 66.2      | 63-72 | 2.00 | 3¾-4¼  |
| Aneiteum                                    |                  |        |         |      |          |          |      |           |       |      |        |
| (ANSP 132647) 1865.....                     | 20               | 3.48   | 3.2-3.9 | 0.15 | 5.5      | 5.0-6.0  | 0.20 | 63.6      | 59-68 | 2.31 | 4-4½   |
| (DMNZ) 1954.....                            | 11               | 3.16   | 3.0-3.3 | 0.09 | 5.2      | 4.8-5.5  | 0.16 | 61.6      | 57-66 | 2.54 | 4-4¾   |

shape was the most found in any New Hebridean helicimid (see Table XII).

Nothing is known about the ecology of *P. varians*. The bright color and trochoidal shape suggest that it may be an arboreal species.

### **Pleuropoma taeniata** (Quoy and Gaimard)

*Helicina taeniata* Quoy and Gaimard, 1832, Voy. Astrolabe, Zool., 2: 194, pl. 12, figs. 6–10—Vanikoro, Santa Cruz Islands; Sowerby, 1847, Thes. Conchy., I, p. 14, pl. 2, figs. 49–51; Pfeiffer, 1846, Syst. Conch. Cab., I, 18, (1), p. 63, pl. A, fig. 14; Sowerby, 1866, Thes. Conchy., 3: 287, pl. 274, figs. 322–323; Sowerby, 1873, Conch. Icon., *Helicina*, pl. 10, figs. 85–86.

*Range*.—Vanikoro Island.

*Material*.—No material available.

*Remarks*.—All of the records in the literature for this species are based on the original description and figures. The figured specimens could not be found in Paris by André Franc, and the only specimens in the Paris Museum labeled *taeniata* did not match the description or figures. Without topotypic material or rediscovery of the type specimens, *taeniata* must remain a dubiously valid species. It is most similar to *P. varians* (Sykes) but differs by having a distinct basal tooth within the columellar lip.

### **Pleuropoma albescens** (Hartman). Plate 26, figs. 5–7, 11.

*Helicina albescens* Hartman, 1890, Proc. Acad. Nat. Sci. Philadelphia, 1890: 285, pl. 3, fig. 5—Segond Channel, Espiritu Santo.

*Range*.—Espiritu Santo.

*Material*.—ML 1, ML 2, ML 31c, ML 31d, ML 31e, ML 31g, ML 32, ML 37a, ML 39, ML 51, ML 66, ML 76a, ML 86, ML 95; Segond Channel, Espiritu Santo (CM 62.15313, ex Hartman, Layard, holotype); New Hebrides (UMMZ 72208, ex Walker).

*Remarks*.—The holotype of *P. albescens* (pl. 26, fig. 5) is a large individual, 7.5 mm. in diameter, 5.7 mm. high, with 4½ whorls. Most specimens (see Table XII) are smaller, differing from the type only in size. *P. albescens* superficially resembles *P. sublaevigata*. On Espiritu Santo, the two species were found at the same collecting site, but apparently they are ecologically isolated, *sublaevigata* living on trees and *albescens* usually under ground debris.

Individuals of *sublaevigata* and *albescens* can be separated by several characters. For convenience they are listed in the following table.

*P. sublaevigata*

1. A strong columellar sinus (see fig. 6).
2. Periphery rounded.
3. Apex flattened.
4. Lip weakly or not reflected.
5. Usually with spiral color bands.
6. Juvenile shells without any hairs.
7. Spire usually convex.
8. Operculum unicolored.

*P. albescens*

1. A weak or no columellar sinus (see fig. 6).
2. Periphery keeled.
3. Apex elevated.
4. Lip strongly reflected.
5. No spiral color bands.
6. Juvenile shells with two or more spiral rows of hairs.
7. Spire usually flattened.
8. Operculum with a red border.

Numbers 1, 2, 4, and 8 are the most useful for identifying adult shells, numbers 1 and 6 for juveniles.

All specimens of *albescens* have a light spiral band on the periphery of the body whorl. The color of the rest of the shell varies from yellow or white to orange and wine-red. The color is not arranged in bands but is distributed over the entire shell in a uniform hue.

The spiral ridges characteristic of *sublaevigata* are also present in *albescens*, although to a much lesser degree. It is suspected that *albescens* and *sublaevigata* may have the same ecological and systematic relationship as the *Trochomorpha rubens* (Hartman) complex. Unlike the latter, however, there is no indication of hybridization between *albescens* and *sublaevigata* in the plantation areas of Espiritu Santo.

***Pleuropoma sublaevigata* (Pfeiffer).** Plate 10, figs. 1–3; plate 26, figs. 12, 13.

*Helicina sublaevigata* Pfeiffer, 1852, Monog. Pneumon. viv., I, p. 384—New Hebrides; Pfeiffer, 1854, Proc. Zool. Soc. London, 1852: 87; Sowerby, 1866, Thes. Conchy., III, p. 290, pl. 274, figs. 339–340; Sowerby, 1873, Conch. Icon., *Helicina*, pl. 29, fig. 265a, b; E. A. Smith, 1884, Proc. Zool. Soc. London, 1884: 268—Api Island; Sykes, 1903, Proc. Malac. Soc. London, 5: 200—Vate, Espiritu Santo, Valua, Vanua Lava, Gaua, Hiu, Lo.

*Helicina layardi* Hartman, 1888, Proc. Acad. Nat. Sci. Philadelphia, 1888: 251, pl. 13, fig. 6—Aore Island; Ancey, 1905, Nautilus, 19, (4), pp. 45–46.

*Helicina novella* Mabilie, 1895, Bull. Soc. d'Hist. Nat. d'Autun, 8: 400–401—New Hebrides (François).

*Helicina bairdi* Reeve, Mabilie, 1895, Bull. Soc. d'Hist. Nat. d'Autun, 8: 401—New Hebrides.

*Orobophana sublaevigata* (Pfeiffer), Wagner, 1905, Denk. Akad. Wien, 77: 426, pl. 7, fig. 17a–c.

*Orobophana sublaevigata layardi* (Hartman), Wagner, 1905, Denk. Akad. Wien, 77: 427, pl. 7, fig. 18.

*Aphanoconia* (*Sphaeroconia*) *sublaevigata* (Pfeiffer), Wagner, 1909, Conch. Cab., I, 18, (2), p. 208, pl. 41, figs. 23–27.

*Palaeohelicina* (*Ceratopoma*) *layardi* (Hartman), Wagner, 1909, Conch. Cab., I, 18, (2), p. 261, pl. 51, figs. 18-22.

*Range*.—Tanna, Vate, Epi, Aore and Espiritu Santo; Valua, Vanua Lava, and Gaua in the Banks; and Hiu and Lo in the Torres.

*Material*.—ML 1, ML 2, ML 26f, ML 31e, ML 32, ML 37a, ML 39, ML 51, ML 66, ML 69, ML 70, ML 76a, ML 86, ML 95; Port Resolution, Tanna (UMMZ 72207, ex Walker); Vate (MCZ 140592, ex Bishop Museum; ANSP 14498, ex Dupuy; CNHM 28627, ex Webb, Ritchie; CM 62.15391, ex Hartman, Layard; ANSP 179794, ex Wolf; UMMZ 72209, ex Walker, Ponsonby, Layard); Vila, Vate (ANSP 133300, ex Froggatt; ANSP 133292, ex Froggatt; Miller 68); Hog Harbour, Espiritu Santo (MCZ 141035, ex J. McMillan); Espiritu Santo (MCZ 113620, ex Bequaert; USNM 432449, 432450, 432451, 432452, ex Harrington; AMNH, ex Banner); Aore (CM 62.15656, ex Hartman, Layard, holotype and paratypes; MCZ, ex W. L. Nutting); New Hebrides (UMMZ 72304, ex Walker, Fulton; ANSP 60914, ex Hartman, Cox).

*Remarks*.—The only extralimital species closely related to *Pleuropoma sublaevigata* (Pfeiffer) is *P. primeana* (Gassies) from the Loyalty Islands and New Caledonia. The two species are very similar in shape, color variations, and size but are easily separated by their different columellar lip margin (see fig. 6). No Solomon Island or Polynesian helicimid is closely related to *sublaevigata* or *primeana*. The Espiritu Santo endemic, *P. albescens* (Hartman), resembles *sublaevigata* but is distinguished by several characters (see above).

A. Wagner (1907-11, pp. 208 and 261) divided *sublaevigata* into two species belonging to two genera. The species were established on the presence (*layardi*) or absence (*sublaevigata*) of spiral ridges on the embryonic whorls. The type specimens of both *layardi* and *sublaevigata* have the spiral ridges. In only 5 per cent of the 575 specimens examined are the ridges completely absent; in many others, however, they are greatly reduced in prominence. Apparently the ridges have no taxonomic value.

The background color of *P. sublaevigata* varies from white to pale yellow, with the latter more common. Most specimens have red supra- and subperipheral color bands. The bands are usually narrower than those found in the syntype (pl. 10, figs. 1, 2). In a few specimens they cover the entire whorl; in others they are split into two fine red lines. Either or both color bands can be absent. In about 15 per cent of the specimens the color bands are unpigmented and are represented by clear, translucent areas in the shell. All vari-

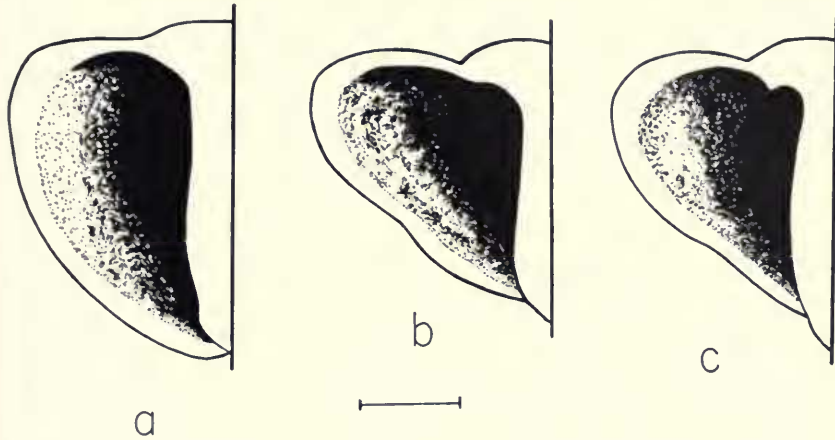


FIG. 6. Umbilical area of *Pleuropoma*. a, *Pleuropoma primeana* (Gassies); Lifu, Loyalty Islands (UMMZ 72122, ex Walker, Ponsonby, Layard). b, *Pleuropoma albescens* (Hartman); Espiritu Santo (ML 32). c, *Pleuropoma sublaevigata* (Pfeiffer); Espiritu Santo (ML 66). Scale line=1 mm.

ations were found in the larger samples. It is suspected that this is the same type of genetically determined polymorphism found in *Bradybaena similis* (Ferussac) by Komai and Emura (1955). Most samples did not contain enough individuals to make tabulation of the different percentages of color forms worth while. In the one large sample (ML 1, with 109 specimens), 35 specimens lacked all bands, 38 had both, 15 had only translucent areas, 7 had no supraperipheral band, 6 had no subperipheral band, 5 had both bands very wide, and 3 had only a very wide subperipheral band.

A few large specimens of *sublaevigata* were more than 8 mm. in diameter, but the majority were much smaller (see Table XII). "*Helicina*" *novella* Mabilie was based on specimens 8–10 mm. in diameter. Although André Franc was unable to locate the types in the Paris Museum, it is suspected that *novella* was based on large specimens of *sublaevigata*. The record for *P. sublaevigata* from Lifu, Loyalty Islands (see Franc, 1957, pp. 34–35, fig. 40) is incorrect, since the figured specimen is quite different from the holotype and the New Hebridean specimens.

Most specimens of *sublaevigata* were collected from the leaves of trees or shrubs, from two to six feet above the ground; a few were collected under debris and logs, and the ecological position of *sublaevigata* needs to be clarified.

**Pleuropoma articulata** (Pfeiffer). Plate 10, figs. 7-9.

*Helicina articulata* Pfeiffer, 1854, Malak. Blätt., 1: 103—Tanna, New Hebrides (April); Pfeiffer, 1854, Proc. Zool. Soc. London, 1853: 53—Tanna, New Hebrides (July); Pfeiffer, 1858, Monog. Pneum. viv., suppl. 1, pp. 191-192; Sowerby, 1866, Thes. Conchy., 3: 294, pl. 12, figs. 409-410; Sowerby, 1873, Conch. Icon., *Helicina*, pl. 26, fig. 236; Sykes, 1903, Proc. Malac. Soc. London, 5: 200—Port Vila, Vate (J. J. Walker).

*Aphanoconia articulata* (Pfeiffer), Wagner, 1908, Conch. Cab., I, 18, (2), p. 162, pl. 32, figs. 1-3.

*Range*.—Tanna, Vate, Aneiteum.

*Material*.—Aneiteum (ANSP 132647, ex Brazier! 1865; DMNZ, W. H. Dawbin!); Vila, Vate (Miller 69, USNM 598362, ex Miller; UMMZ 72115, ex Walker, Ponsonby, Sykes); Vate (UMMZ 72116, ex Walker, Layard; UMMZ 72199, ex Walker, Layard, Garrett; CM 62.15338, ex Hartman, Layard; DMNZ, W. H. Dawbin!); New Hebrides (UMMZ 72114, ex Walker; AMNH; MCZ; CNHM 28729, ex Webb, Sowerby; CNHM 28820, ex Webb, Sowerby).

*Remarks*.—*Pleuropoma articulata* is quite variable in color pattern, degree of carination, and sculpture. There are two different color patterns. Most specimens (pl. 10, figs. 7-9) have the middle of each whorl clear and slightly translucent with the alternating red and white flammulations confined to the periphery and areas bordering the sutures. In some the zigzag pattern is continuous over the entire whorl, as in *fulgora* Gould, *zebriolata* Pfeiffer, and *suturalis* von Martens. In most shells the stripes are absent on the base of the shell, but in a few specimens they continue to the umbilical callus. Many specimens of intermediate aspect were seen. Acutely carinated, obtusely keeled (pl. 10, fig. 8) and intermediate shells were also found. Narrow spiral ridges, arising from a deciduous periostracum, are present in some shells but are totally absent or partially eroded in the majority.

The Vate and Aneiteum populations differ in size and degree of carination (see Table XII). The Aneiteum population closely approximates the type figures of *P. zebriolata* (Pfeiffer) (see p. 179), and perhaps the name should be applied to the Aneiteum shells rather than the supposed Samar (Philippine Islands) population. In view of the uncertainty of the reference of the name *zebriolata*, the uncertainty of the importance of the variation between the Vate and Aneiteum populations, and the complexity of the entire "zonata" group (see below), I have not given taxonomic recognition to the Aneiteum population.



It is interesting to note the differences between the populations collected in different years on Vate and Aneiteum (see Table XII). There is, of course, little probability that the identical local populations were sampled at the two times, but the size differences between the two sets illustrates the unreliability of size as a valid character in separating species of land prosobranchs.

The characters mentioned in the preceding paragraph have been used to separate the many small heliciniids related to *articulata*. The range of variation shown by the New Hebridean shells encompasses most of the named taxa. E. A. Smith (1897, p. 522) previously suggested that several of the "species" are probably synonymous. In none of the "species" have the soft parts been examined and only in Hawaii have local colonies of these heliciniids been sampled and compared (see Neal, 1934, pp. 39-78). It would be very unusual if only one species could be recognized over the entire Pacific, but certainly many of the names in current use will be discarded when the entire complex is studied in detail.

A probably incomplete list of "species" closely related to *articulata* includes the following "*Helicina*": *zonata* Lesson, 1830, *zigzag* Pease, 1867, and *ponapensis* Wagner, 1911, from the Caroline Islands; *suturalis* von Martens, 1864, from the Moluccas; possibly *zebriolata* Pfeiffer, 1855, from the Philippines; *gallina* Gassies, 1870, and *mariei* Crosse, 1870, from New Caledonia; *vicina* Wagner, 1911, from Fiji; *fulgora* Gould, 1847, *musiva* Gould, 1847, *brenchleyi* Baird, 1873, and *altivaga* Ancey, 1889, from Samoa; *flammea* Quoy and Gaimard, 1832, and *diminuta* Mousson, 1871, from Tonga; *oceanica* Pease, 1867, from the Gilbert Islands; and *laciniosa* Neal, 1934 (not Mighels, 1845), *oahuensis* Pilsbry and Cooke, 1908, *nonouensis* Neal, 1934, and *subsculpta* Neal, 1934, from the Hawaiian Islands. Many specimens of the above "species" are in the University of Michigan Museum of Zoology. The Hawaiian, Moluccan, and Gilbert Island shells are easily separated from the New Hebridean, but the great majority of the others are very similar.

### **Pleuropoma rotella** (Sowerby). Plate 10, figs. 4-6.

*Helicina rotella* Sowerby, 1847, *Thes. Conchy.*, I, p. 12, pl. 3, figs. 135-136—locality unknown; Pfeiffer, 1852, *Monog. Pneum. viv.*, I, p. 387; Pfeiffer, 1858, *op. cit.*, II, p. 109—Tanna, New Hebrides; Sowerby, 1866, *Thes. Conchy.*, 3: 291, pl. 275, fig. 358—New Hebrides; Sowerby, 1873, *Conch. Icon.*, *Helicina*, pl. 12, fig. 104.

*Range*.—Tanna.

*Material*.—Photograph of holotype (BM).

*Remarks.*—Identification of the Tanna shells (probably collected by MacGillivray) with *Helicina rotella* needs confirmation. The only heliciniids from Tanna examined during this study (UMMZ 72207) were slightly atypical *sublaevigata*. *P. rotella* differs from *sublaevigata* in having a more sharply angulated periphery and an expanded lip. In this respect, as well as in color variation, *rotella* resembles the Espiritu Santo *albescens*. The latter is substantially smaller than *rotella* (which is 9–11 mm. in diameter) and has a less indented columellar sinus.

The following three species, described from the New Hebrides, probably were from other areas. *P. subreticulata* (Wagner) and *Sturanyella modesta* (Pfeiffer) almost certainly are extralimital, but *Pleuropoma zebriolata* (Pfeiffer) may be a synonym of *P. articulata* (Pfeiffer).

#### **Sturanyella modesta** (Pfeiffer)

*Helicina modesta* Pfeiffer, 1854, Proc. Zool. Soc. London, 1853: 52—Tanna, New Hebrides; E. A. Smith, 1885, op. cit., 1885: 598–599—Shortland, Treasury, and Guadalcanal Islands in the Solomons.

*Sturanya modesta* (Pfeiffer), A. J. Wagner, 1907, Conch. Cab., I, 18, (2), p. 43, pl. 6, figs. 25–29; I. and B. Rensch, 1936, Rev. Suisse Zool., 43, (32), p. 683—New Georgia; Dell, 1955, Pacific Science, 9, (3), p. 325—Nissan Island, northern Solomons.

*Range.*—Solomon Islands.

*Material.*—Many lots in the collection of the University of Michigan Museum of Zoology.

*Remarks.*—The identity of Cuming's types with Solomon Island specimens was established by E. A. Smith. *Helicina modesta*, type locality Tanna, New Hebrides, is "No. 19" in Pfeiffer's list of new species. "No. 18" in the same list is *Pupina cumingiana* Pfeiffer, type locality Solomon Islands, which has only been found on Tanna in the New Hebrides (see p. 189). It is very probable that the localities were accidentally transposed. No shell resembling *S. modesta* is known from the New Hebrides, and I have not accepted the species as part of the fauna.

#### **Pleuropoma subreticulata** (Wagner)

*Aphanoconia* (*Sphaeroconia*) *subreticulata* A. J. Wagner, 1909, Conch. Cab., I, 18, (2), pp. 196–197, pl. 40, figs. 5–9—New Hebrides.

*Range.*—Queensland.

*Material.*—Queensland (UMMZ 72212, ex Walker, Rolle, cotype).

*Remarks.*—Wagner compared *P. subreticulata* to the Australian *P. gouldiana* (Forbes), noting only a very few minor differences. The presence of a cotype in the collection (UMMZ) from Queensland, where *P. gouldiana* lives, makes it very probable that the New Hebridean locality for *subreticulata* is an error in Wagner's monograph.

### **Pleuropoma zebriolata** (Pfeiffer)

*Helicina zebriolata* Pfeiffer, 1855, Proc. Zool. Soc. London, 1855: 101–102—Lord Howe Island (error); Pfeiffer, 1858, Monog. Pneum. viv., suppl. 1, p. 191; Sowerby, 1866, Thes. Conchy., 3: 294, pl. 12, figs. 407, 408—Samar, Philippine Islands; Sowerby, 1873, Conch. Icon., *Helicina*, pl. 26, fig. 229.

*Geophorus* (?) *zebriolata* (Pfeiffer), Faustino, 1930, Philippine Jour. Sci., 42, (1), p. 174.

*Range.*—Samar, Philippine Islands.

*Material.*—Samar (UMMZ 72062, ex Walker, Ponsonby, Melville).

*Remarks.*—No helicinids live on Lord Howe Island (Iredale, 1944) and the original locality is thus an obvious error. Sowerby's identification of *zebriolata* with the Samar shells is here accepted with some reservations. The coloration and size of *zebriolata* are the same as the large, sharply keeled variety of *Pleuropoma articulata* (Pfeiffer). Study of the types of *zebriolata* may result in its being added to the synonymy of *articulata* instead of being referred to the Samar shells. Moellendorff (1897, pp. 179–182) did not include *zebriolata* among the Philippine Island Helicinidae, although the record for Samar had been published more than thirty years prior to his study. It is thus possible that Samar may be another erroneous locality.

## Order MESOGASTROPODA

### Suborder ARCHITAENIOGLOSSA

#### Superfamily CYCLOPHORACEA

Aside from the systematic compilation of Kobelt (1902b), no family-wide studies of the Cyclophoracea have appeared since those of L. Pfeiffer in the middle 1800's. In recent years systems of classification have been proposed by Thiele (1929), Wenz (1938–44), Tielecke (1940), Torre, Bartsch and Morrison (1942), and Morrison (1955). Thiele's and Wenz's systems were only slightly changed from Kobelt's, but the others proposed important modifications. In establishing higher categories Tielecke relied on the structures of the

central nervous system, male and female genitalia, and pallial region, Torre, Bartsch and Morrison on the shell and operculum, and Morrison on the external male reproductive organs. Differences between the classifications are numerous and fundamental. None is fully satisfactory, but that of Tielecke probably has the soundest basis, in that several organ systems are used as diagnostic characters. For this reason, Tielecke's family divisions have been accepted here (see also van Benthem Jutting, 1948).

Three of Tielecke's five families, the Poteriidae (fig. 16), Pupiniidae (fig. 14), and Diplommatinidae (=Cochlostomatidae) (fig. 17), are found in the New Hebrides. The Cyclophoridae are common in Indonesia and reach the Solomons. The fifth family, Maizaniidae, is endemic in Africa.

Because of the unsettled classification, no attempt has here been made to characterize suprageneric taxa.

#### Family POTERIIDAE

Tielecke's family Poteriidae is equivalent to the subfamily Poteriinae of Thiele (1929, pp. 102-103) with the addition of *Ostodes* and related Pacific genera (see Clench, 1949, pp. 4-29). Despite conchological differences, the genital tracts and nervous systems show that these Oceanic and Neotropical genera are more closely related to each other than to any other cyclophoraceans (see Tielecke, 1940, pp. 361-363). Further study may warrant subfamily recognition for the Pacific genera, and it is also possible that the African Maizaniidae may prove to be a closely related group.

Morrison (1955) does not consider the Pacific cyclophoraceans, but it is worth while to contrast his classification of the American poteriine genera with Tielecke's single family:

- Family Cyclophoridae
  - Subfamily Cyclophorinae
    - Genus *Buckleyia*
  - Subfamily Neopupiniinae
    - Genus *Aperostoma* (= *Cyrtotoma*)
  - Subfamily Neocyclotinae
    - Genus *Poteria*
    - Genus *Neocyclotus*
- Family Amphicyclotidae
  - Genus *Amphicyclotus*
  - Genus *Crocidopoma*

Morrison's families and subfamilies are based on the structure of the male verge, an organ which is quite variable in land Mollusca. The verge is very useful in systematics, but too much importance can be attached to it, as well as to the shell and the operculum.

Clench (1949, pp. 4-29) revised the Pacific Poteriidae, basing the seven genera (five new) on opercular characters. The only "cyclophorid" not mentioned in his study is *Cyclostoma obligatum* Gould, 1852, from Tahiti. Examination of a specimen (UMMZ 85675) showed that it belongs to the assimineid genus *Cyclomorpha*. The relation of the New Zealand endemics, *Liarea* and *Murdochia*, to the other Pacific cyclophorids is uncertain. The reproductive anatomy of *Liarea* is unknown, while the only study on *Murdochia* (Morton, 1952) does not offer sufficient information for a detailed comparison with the other Pacific genera. The radulae of *Murdochia* (Morton, 1952, pl. 25, fig. 4) and *Liarea* (Powell, 1954, pl. 48, figs. 38-40) are quite different from those of the Polynesian cyclophoraceans figured by Clench (1949, p. 48, fig. 28), but so few cyclophorid radulae have been studied that the importance of the differences is unknown.

According to Morton (1952, pp. 76-77) the oviduct of *Murdochia* enters the receptaculum seminalis, which opens into the uterus (pallial oviduct). No mention is made of the bursa copulatrix. It is impossible to compare the female organs of *Murdochia* with the species studied by Tielecke (1940) without knowing the position of the bursa; the point where the oviduct enters the uterus; and the relation between the bursa and receptaculum.

Both males and females of *Ostodes strigatus* (Gould) were dissected by Tielecke (1940, pp. 331-332). Females of *Ostodes adjunctus* (Mousson) and both sexes of *Gonatoraphe fornicata* (Pfeiffer) were available for this study. The female anatomy of the three species differed only in minor details. The external male organ of *Ostodes strigatus* is located mid-dorsally and well behind the tentacles. It consists of a large, rugose, fleshy verge with narrow terminal appendage. There is a distinct sperm furrow running from the end of the vas deferens to the tip of the penial appendage. The shape and location of the verge in *Gonatoraphe fornicata* (pl. 6, fig. 10) are the same, but *G. fornicata* differs in having the sperm furrow closed to form an internal, tubular "vas" running from the pallial genital pore to the tip of the cephalic penis. In *Murdochia* (Morton, 1952, pp. 75-76, fig. 2) the penis is lateral and attached behind the right tentacle. There is a

tubular vas deferens, and the tip has developed into a retractile intermittent organ.

According to the criteria of Morrison (1955), *Ostodes* would belong to the subfamily Neocyclotinae of the Cyclophoridae, *Gonatoraphe* to the Amphicyclotidae, and *Murdochia* to the cyclophorid subfamily Neopupininae. The transition from a seminal groove to a tubular vas deferens is probably only of generic value and not indicative of family affinities in the Cyclophoracea.

Until the anatomy of the New Caledonian *Gassiesia* and Fijian *Gonatoraphe* is known, the relationship between *Gassiesia*, *Gonatoraphe*, and *Ostodes* will be uncertain. The shell of *Gonatoraphe* is transitional in shape and sculpture between *Gassiesia* and *Ostodes*. The latter two have horny operculi but the operculum of *Gonatoraphe* is heavily calcified. The importance of the opercular and vergic differences and the affinities of *Fijipoma* and the Caroline Island *Paramia* and *Kondoraphe* cannot be determined at present. I suspect that the Pacific Poteriidae are relicts which have been replaced in Indonesia and northern Melanesia by the cyclophorine genera *Lagochilus* and *Leptopoma*, and that *Gassiesia* and *Ostodes* will be found to be primitive relatives of *Gonatoraphe*.

The anatomical information given by Tielecke (1940) and the results of this study enable modification of the generic descriptions in Clench (1949). Expanded generic definitions are given below, not only for the Fijian–New Hebridean *Gonatoraphe*, but also for the Samoan *Ostodes*, and the New Caledonian *Gassiesia*.

### Genus **OSTODES** Gould, 1862

Shell globose to depressed-turbinate, solid, and opaque. Surface with spiral lirae (except *O. cookei* Clench) and, in many species, broad, flattened axial plicae. Umbilicus wide, body whorl rounded or acutely keeled. Operculum horny, multispiral, with depressed nucleus. Male verge external, mid-dorsal, posterior, with open seminal groove and terminal appendage. Oviduct, seminal receptacle, and bursa copulatrix opening into uterus through a single pore. (Modified from Tielecke, 1940, pp. 331–332, and Clench, 1949, p. 9.)

*Type species*.—*Cyclostoma strigatum* Gould.

*Range*.—Savaii, Upolu, and Tutuila, Samoa.

### Genus **GONATORAPHE** Moellendorff, 1898

Shell depressed turbinate, solid, widely umbilicate. Sculpture of spiral lirae, most species with broad axial plicae. Operculum flat, calcareous, multispiral, with depressed nucleus. Male verge external, mid-dorsal, posterior, with internal tubular ejaculatory duct. Oviduct, seminal receptacle, and bursa copulatrix opening into uterus through a single pore. (Modified from Clench, 1949, p. 18.)

*Type species.*—*Cyclostoma recluzianum* Pfeiffer (= *fornicatum* Pfeiffer).

*Remarks.*—Thiele (1928a, p. 128, and 1929, p. 173) placed *Gonatoraphe* in the Assimineidae, but the radula, operculum, and anatomy prove that it is a cyclophoracean. Clench (1949, pp. 18–23) described and figured the three Fijian species and summarized previously published data on the New Hebridean representatives. My study of 250 New Hebridean specimens indicated that only one species is found on the islands.

**Gonatoraphe fornicata** (Pfeiffer). Plate 6, figs. 9, 10; plate 9, figs. 4–6; plate 26, figs. 1, 2.

*Cyclostoma (Cyclophorus) fornicatum* Pfeiffer, 1854, Proc. Zool. Soc. London, 1852: 146—New Hebrides (Cuming).

*Cyclostoma (Cyclotus) recluzianum* Pfeiffer, 1854, Proc. Zool. Soc. London, 1853: 51—Solomon Islands (Cuming) (corrected to New Hebrides by Brazier, 1871, p. 587).

*Cyclostoma fornicatum* Pfeiffer, 1854, Conch. Cab., I, 19, p. 376, pl. 49, figs. 6–8.

*Cyclostoma (Cyclotus) macgillivrayi* Pfeiffer, 1855, Proc. Zool. Soc. London, 1855: 103–104—Aneiteum (MacGillivray).

*Cyclophorus fornicatus* Pfeiffer, 1861, Conch. Icon., *Cyclophorus*, pl. 18, fig. 86a, b; Cox, 1868, Exchange List, p. 49, no. 196—New Hebrides.

*Cyclotus recluzianus* Pfeiffer, 1863, Conch. Icon., *Cyclotus*, pl. 9, fig. 53; Cox, 1868, Exchange List, p. 49, no. 193; Brazier, 1871, Proc. Zool. Soc. London, 1871: 587—restriction of type locality to Dillon's Bay, Erromanga.

*Cyclotus macgillivrayi* Pfeiffer, Cox, 1868, Exchange List, p. 49, no. 192—Aneiteum; Brazier, 1871, Proc. Zool. Soc. London, 1871: 587—Aneiteum.

*Cyclotus charmian* Hutton, 1883, Trans. New Zealand Inst., 16: 209—Horoiki, Wellington, New Zealand (error); Suter, 1913, Man. New Zealand Moll., p. 684—synonymizes with *macgillivrayi* Pfeiffer.

*Cyclophorus vieillardii* Mabile (not Gassies), 1895, Bull. Soc. d'Hist. Nat. d'Autun, 8: 401—New Hebrides (François).

*Ostodes fornicata fornicata* (Pfeiffer), Sykes, 1903, Proc. Malac. Soc. London, 5: 199—Vila, Vate.

*Ostodes fornicata* var. *macgillivrayi* (Pfeiffer), Sykes, 1903, Proc. Malac. Soc. London, 5: 199—Vila, Vate and Renee River, Espiritu Santo.

*Gonatoraphe fornicata fornicata* (Pfeiffer), Clench, 1949, Bull. B. P. Bishop Mus., 196: 19–20.

*Gonatoraphe fornicata macgillivrayi* (Pfeiffer), Clench, 1949, Bull. B. P. Bishop Mus., 196: 20.

*Range.*—Aneiteum, Erromanga, Vate, Espiritu Santo.

*Material.*—ML 59, ML 70, ML 72, ML 76a; Erromanga (USNM 515694, ex Chamberlain, Calvert; ANSP 13398, ex Wilstach); Anei-

teum (ANSP 132659, Brazier!); Vila, Vate (ANSP 133299, Froggatt!; USNM 598355, ex W. B. Miller; Miller 108); Vate (UMMZ 74393, ex Walker, Ponsonby); Vate and Aneiteum (UMMZ 74391, ex Walker, Ponsonby, Layard); Renee River, Espiritu Santo (UMMZ 74390, ex Walker, Ponsonby, Sykes, J. J. Walker!); New Hebrides (UMMZ 74389, ex Walker, Ponsonby; CNHM 32431, ex Webb, Sowerby and Fulton).

*Remarks.*—The conclusion of Sykes (1903, p. 199) that the three named "species" are inseparable is confirmed by the type photographs (pl. 9, figs. 4–6). As was suspected from the original measurements, *fornicata* (pl. 9, fig. 6) is based on very juvenile specimens, which have a much sharper keel than adult material, and variety *recluziana* is also a juvenile (pl. 9, fig. 4), with only a slightly less prominent keel than *fornicata*. Most adult specimens are close to *macgillivrayi* (pl. 9, fig. 5), except that gerontic individuals (pl. 26, figs. 1, 2) have a much higher spire and a somewhat deflected aperture. Typologically, then, *fornicata*, *recluziana* and *macgillivrayi* represent growth stages, rather than different taxonomic entities. The populations from Aneiteum and Erromanga are not separable, although Brazier (1871, p. 587) considered that they were different.

The specimens differed only in size and whorl count, since the sculpture, whorl increase, height of spire, umbilicus and degree of carination showed the same variations in each population. Specimens from Vate were very small (diameter 7.1 mm.,  $4\frac{1}{8}$  whorls), those from Aneiteum and Erromanga were intermediate (diameter 9.5 mm.,  $4\frac{1}{2}$  whorls), and those from Espiritu Santo (Lot ML 72, collected alive) were large (diameter 11.1 mm.,  $4\frac{7}{8}$  whorls). The size and whorl count differences are probably not taxonomically important, but are the result of differing ecological conditions. Land operculates are quite sensitive to lack of moisture, and examples of stunted populations in ecologically unfavorable areas are numerous (see van der Schalie, 1948, pp. 26–30).

The sculpture varied in the prominence, spacing, and number of lirae as well as in the number of longitudinal plications. In the latter respect, gerontic shells from Espiritu Santo (pl. 26, figs. 1, 2) were quite similar to *Gonatoraphe stricta* (Garrett) from Fiji. The sculpture was not constant within a lot, nor could height of spire and umbilical variations be used to separate populations.

Several animals of *G. fornicata* were dissected. Male and female genitalia are figured (pl. 6, figs. 9, 10). In preserved specimens, the



reflexed portion of the female oviduct was bound to the seminal receptacle by connective tissues and the bursa was appressed against the kidney. The organs are shown in unnatural positions to indicate their relative sizes and the points at which they connect with each other. The diagram of the external male organ shows the position of the verge with the mantle slit. The dotted line indicates the path of the ejaculatory duct. Several radulae were examined and found to be the same as that of *G. stricta* (Garrett) figured by Clench (1949, p. 48, fig. 28c). The teeth have not been figured here.

### Genus *GASSIESIA* Clench, 1949

Shell depressed-turbinate, solid, widely umbilicate. Sculpture of weak spiral threads; some species with an axial sculpture of growth lines. Operculum horny, multispiral, with depressed nucleus. Male with medially placed dorsal verge. (Modified from Clench, 1949, p. 5.)

*Type species*.—*Cyclostoma artense* Montrouzier.

*Remarks*.—The information on the position of the verge is taken from Fischer and Crosse (1880–1902, p. 137) and refers to *G. montrouzieri* (Souverbie). One species, *Gassiesia forbesianus*, was described from "Lord Howe's Island, New Hebrides." The species probably is based on a mislabeled New Caledonian shell.

### *Gassiesia forbesianus* (Pfeiffer)

*Cyclostoma (Cyclophorus) forbesianus* Pfeiffer, 1856, Proc. Zool. Soc. London, 1855: 104—Lord Howe Island, New Hebrides (MacGillivray!) (error).

*Cyclophorus forbesianus* Pfeiffer, 1858, Monog. Pneum. viv., II, p. 63; Pfeiffer, 1861, Conch. Icon., *Cyclophorus*, sp. 72.

*Ostodes forbesianus* (Pfeiffer), Kobelt, 1902, Das Tierreich, 16: 155—Santa Cruz Islands.

*Gassiesia forbesianus* (Pfeiffer), Clench, 1949, Bull. B. P. Bishop Mus., 196: 6–7.

*Range*.—New Caledonia or Isle of Pines(?).

*Material*.—New Hebrides (UMMZ 85670, ex Walker, Ponsonby; ANSP 12860, ex Swift, Cuming, cotypes?).

*Remarks*.—Clench (1949, p. 6) tentatively equated *forbesianus* with the New Caledonian *bocageanus* Gassies. Probably this is correct, but until types can be compared and adequate collections made in New Caledonia and the Santa Cruz Islands, the type locality and identity of *forbesianus* will remain uncertain. The operculum of the ANSP cotypes(?) is like the New Caledonian *Gassiesia* rather than the opercular type of *Gonatoraphe*.

## Family PUPINIDAE

The two subfamilies, Pupininae and Pupinellinae, are easily separated by differences in anatomy (see Tielecke, 1940, p. 366) and the dull, radially sculptured pupinellids are quite different from the smooth, glossy shells of the pupinids. Pupinellids range from Asia to the Louisiades and Australia, but do not reach the Solomons. The subfamily Pupininae reaches its eastward limit in the New Hebrides and Fiji.

## Subfamily PUPININAE

Species assignable to the Pupininae are found in India, China, Java, and the Philippines, and throughout most of Micronesia and Melanesia. Apparently they do not reach the Marianas, Polynesia, New Caledonia, New Zealand,<sup>1</sup> or Australia south of northern New South Wales (fig. 14). Numerous generic and subgeneric names, based on the size, shape, and number of apertural notches, have been proposed (see Kobelt, 1902b, pp. 301–336; Iredale, 1937a, pp. 295–299; and Clench, 1949, pp. 30–48). Similar apertural configurations are found in specimens from widely separated regions, but it is unknown whether these variations are phyletic or convergent. Although lack of both material and time has prevented more than cursory review of the classification, I have restudied the Melanesian and Micronesian species and have tentatively subordinated Iredale's genera to previously known taxa. Dr. William J. Clench has been most helpful in permitting me to study the extensive series in the Museum of Comparative Zoology and in making suggestions about this difficult group.

After separating a few specialized taxa—*Hargravesia*, *Moulinsia*, *Porocallia*, *Callianella*, and *Pupinoa*—most workers divide the remaining Pupininae into two large and widely distributed genera, *Pupina* and *Tylotoechus*. As Clench (1949, p. 44) stated, many species are easily placed, but others are intermediate. Without an extensive revision, their true relationship is uncertain. For convenience, I have here maintained the historical status quo. The New Hebridean species belong to *Pupina*.

Acting on his usual assumption that any Australian species is, ipso facto, generically different from any non-Australian species, Iredale (1937a, pp. 295–299) created several new "genera" for the Queensland and New South Wales pupinids. All seem closely related and

<sup>1</sup> *Liarea* (or *Realia*) from New Zealand (see Powell, 1954) has been placed in the Pupininae, but its affinities are uncertain.

are probable derivatives of *Pupina* (sens. str.). The Australian species are considered to be a subgenus of *Pupina*, called *Signepupina* Iredale, 1937. Of Iredale's other "genera," *Estopupina* and *Necopupina* are probably sections of some pupinelline genus, while *Lopupina*, *Diplopupina*, *Parpupina* and *Dolopupina* represent evolutionary developments from *Signepupina* of not more than sectional value.

#### Genus PUPINA Vignard, 1829

Species from the Philippines (*gracilis* Moellendorff) and Australia (*pfeifferi* Dohrn) are similar enough to the genotype, *P. keradreni* Vignard, to be included in the same genus. The Australian species belong to a subgenus, *Signepupina*, while typical *Pupina* includes the island species from the Philippines to the Fijis.

#### Subgenus PUPINA (sens. str.)

Although a few Philippine Island species probably belong to *Pupina* (sens. str.), this discussion is limited to the Micronesian and Melanesian species. The species of New Guinea and northern Melanesia have both a well-developed parietal tooth and a columellar notch. In the island chains fanning out from this core, it is possible to trace three parallel lines of development. In the Palau Islands, *P. difficilis* Semper is quite close to *P. keradreni*, but *P. brenchleyi* E. A. Smith from Lukunor and *P. complanata* (Pease) from Kusaie in the Carolines show a gradual reduction in the size of the parietal notch. The Fijian species (*Pupinesia* Clench, 1949, p. 39) have lost the parietal notch, and the columellar notch has been considerably modified. The New Hebridean species (*Kanapa* Clench, 1949, p. 41) lack a prominent parietal notch, although retaining the columellar notch. *Pupinesia* and *Kanapa* represent obvious offshoots of *Pupina* only slightly more differentiated than the Palau-Caroline Island series. Their *relationships* are much more clearly shown by making *Kanapa* and *Pupinesia* sections of *Pupina* rather than distinct genera.

#### Section KANAPA Clench, 1949

Similar in general shell outline to *Pupina*, s. s., but differs in lack of a parietal notch and parietal tooth. Columellar notch is small but enlarged somewhat beneath lip margin (Clench, 1949, p. 41).

*Type species*.—*Registoma brazieri* Crosse.

*Remarks*.—Of the three species Clench placed in *Kanapa*, *P. brazieri* and *P. cumingiana* are from the New Hebrides; the third,

*P. manni* (Clench), is from Three Sisters Island in the Solomons. Probably it is only a local development from *Pupina keradreni* Vignard, since the columellar structure of *manni* is like that of *keradreni* rather than that of the New Hebridean *Kanapa*.

Table XIII.—Size Variation in the New Hebridean *Pupina*

|  | Height |         | Diameter |         | H/D  |         |
|--|--------|---------|----------|---------|------|---------|
|  | Mean   | Range   | Mean     | Range   | Mean | Range   |
| <i>P. cumingiana</i> .....<br>(MCZ 140552) | 9.1    | 8.0-9.7 | 3.7      | 3.3-4.1 | 2.4  | 2.2-2.7 |
| <i>P. cumingiana</i> .....<br>(ANSP 13167) | 8.3    | 8.0-8.6 | 3.6      | 3.3-3.9 | 2.3  | 2.2-2.5 |
| <i>P. brazieri</i> .....                   | 6.0    | 5.8-6.3 | 3.0      | 2.9-3.2 | 2.0  | 1.9-2.1 |

*P. brazieri* has no trace of a groove at the parietal angle, while *P. cumingiana* has either a weak groove or a prominent notch. Generally, *brazieri* is much smaller (5.8-6.3 mm.) than *cumingiana* (8.0-9.7 mm.), but a few dwarf specimens of *cumingiana* (6.5-9.7 mm.) were seen.

#### ***Pupina* (*Kanapa*) *brazieri* (Crosse)**

*Registoma complanatum* Cox (not Pease), 1868, Exchange List, p. 50, no. 210—Erromanga.

*Registoma brazieri* Crosse, 1870, Jour. de Conchy., 18: 250-251—Erromanga; Crosse, 1871, Jour. de Conchy., 19: 321-322, pl. 13, fig. 6.

*Pupina* (*Pupina*) *brazieri* (Crosse), Kobelt, 1902, Das Tierreich, 16: 302.

*Kanapa brazieri* (Crosse), Clench, 1949, Bull. B. P. Bishop Mus., 196: 42-43, figs. 23b, 24a.

*Range*.—Erromanga, Espiritu Santo.

*Material*.—ML 95; Erromanga (MCZ 14109, ex Beddome, Brazier; MCZ 141008, ex Pease, Brazier; UMMZ 87408, ex Walker, Ponsonby, Beddome, Brazier); New Hebrides (ANSP 13177, ex Wilstach; UMMZ, ex Walker, Ponsonby; MCZ 141010, ex Dohrn; MCZ 141011).

*Remarks*.—The small (5.8-6.3 mm.) size and compressed spire of *P. brazieri* at once separate it from *P. cumingiana*. Unlike the latter species, *P. brazieri* had no trace of an apertural notch in any of the specimens I saw. The Espiritu Santo shells are inseparable from the syntypes in the Museum of Comparative Zoology. The holotype and four paratypes are preserved in the collection of the Journal de Conchyliologie in Paris (see Jour. de Conchy., 90: 77).

**Pupina (Kanapa) cumingiana** Pfeiffer. Plate 9, fig. 8.

*Pupina (Pregistoma)* (sic) *cumingiana* Pfeiffer, 1853, Proc. Zool. Soc. London, 1853: 52—Solomon Islands (error).

*Registoma cumingiana* (Pfeiffer), 1858, Monog. Pneum. viv., II, p. 97—Lord Howe's Island (MacGillivray) (error); Cox, 1868, Exchange List, p. 50, no. 211.

*Registoma cumingiana minor* Pfeiffer, 1865, Monog. Pneum. viv., suppl. 3, p. 97—New Caledonia (error).

*Pupina (Registoma) cumingianum* Pfeiffer, 1876, Monog. Pneum. viv., suppl. 4, p. 152—Tanna.

*Pupina (Pupina) cumingianum* Pfeiffer, Kobelt, 1902, Das Tierreich, 16: 303.

*Pupina cumingiana* Pfeiffer, Sykes, 1903, Proc. Malac. Soc. London, 5: 200—Resolution Bay, Tanna (J. J. Walker).

*Kanapa cumingiana* (Pfeiffer), Clench, 1949, Bull. B. P. Bishop Mus., 196: 43–44, fig. 23c.

*Kanapa cumingiana minor* (Pfeiffer), Clench, 1949, op. cit., p. 44.

*Range.*—Tanna.

*Material.*—Tanna (UMMZ 87824, ex Walker, Ponsonby; MCZ 140551, ex Bishop Museum, Brazier, MacGillivray, cotypes; MCZ 140552, ex Bishop Museum, E. Robertson! July, 1925; MCZ 165719, ex Boston Soc. Nat. Hist., Geale; ANSP 13167, ex Brazier); New Hebrides (UMMZ 161465, ex Walker; UMMZ 87507, ex Walker, Ponsonby); erroneous localities (UMMZ 13155, ANSP 13165, ANSP 13166, ANSP 13164, ANSP 13163).

*Remarks.*—Most specimens of *cumingiana* are the size and shape of the holotype (pl. 9, fig. 8), but those collected by Robertson in 1925 (MCZ 140552) are much more elongate. Comparative measurements of *cumingiana* and *brazieri* are given in Table XIII.

All specimens of *cumingiana* have an *internal* parietal groove but show a great variation in the extent of development of the parietal notch. In the holotype and about one-third of the specimens, the notch is absent. In others it is partially developed, and in one specimen (UMMZ 87824) the notch is as fully developed as in *P. complanata* Pease (UMMZ 87501, 87502, 87503 and 87504; see also Clench, 1949, p. 34, fig. 20c). The "notched" *ponsonbyi* and the "notchless" *cumingiana* intergrade fully and cannot be separated. The presence of a variety of *cumingiana* with a parietal notch weakens the validity of *Kanapa*, but it can still be retained as a useful indicator that the New Hebridean species are different from, although closely related to, the Solomon Island *Pupina*. A lot (UMMZ 87507) of dwarf *P. cumingiana* contained one small specimen 6.5 mm. in height and five others ranging from 7.1–7.4 mm.

## Family DIPLOMMATINIDAE

The family group name Diplommatinidae must replace the name Cochlostomatidae (Tielecke, 1940, p. 364), since the former dates from L. Pfeiffer in 1856 (Malak. Blätt., 3: 118). Two subfamilies are usually recognized, the European Cochlostomatinae and the Indo-Pacific Diplommatininae. Possibly the Central American *Adelopoma* should be placed with the Diplommatininae.

Of the many genera in the Diplommatininae (fig. 17), only *Palaina*, *Diplommatina*, *Diancta*, *Pseudopalaina*, and the monotypic *Hungerfordia* reach the islands of the Pacific, excluding the Philippines and Indonesia. *Palaina* occurs in the Palau, Caroline, and Mariana Islands of Micronesia, all of Melanesia, Lord Howe and Norfolk Islands, and east to Tonga; *Diplommatina* in Fiji, Samoa, and the Solomons; *Diancta* in Fiji; and *Pseudopalaina* and *Hungerfordia* in the Palau Islands.

All genera are based on shell characters only. *Palaina* includes species without a parietal tubercle and *Diplommatina* species with a parietal tubercle. Some species can be placed in either genus (Solem, in press-A), but the New Hebridean species are unquestionably *Palaina*. Excellent figures showing the variation found in the Diplommatininae are given by Zilch (1953).

## Genus PALAINA O. Semper, 1865

*Type species*.—*Diplommatina macgillivrayi* Pfeiffer by subsequent designation of Iredale (1944, p. 303).

*Remarks*.—Several subgeneric names, based on shell contour, have been proposed. Probably these names identify convergent evolution, since similarly shaped shells are found in all parts of the range of the genus. A list of these nomenclatural units is included for future reference. All type species are by original designation.

**Eupalaina** Kobelt and Moellendorff, 1898

An absolute synonym of *Palaina* (sens. str.).

**Cylindropalaina** Moellendorff, 1897

*Type species*.—*Palaina chrysalis* Moellendorff.

**Macropalaina** Moellendorff, 1897

*Type species*.—*Palaina pomatiaeformis* Mousson.

**Eclogarinia** Iredale, 1933

*Type species*.—*Diplommatina gowlandi* Brazier.

**Velepaina** Iredale, 1937

*Type species*.—*Diplommatina oreadis* Hedley.

**Palmatina** Iredale, 1944

*Type species*.—*Diplommatina coxi* H. Adams.

**Fermepalaina** Iredale, 1945

*Type species*.—*Palaina nancena* Iredale.

Many papers have appeared on the Austro-Melanesian *Palaina*. The important sources for information are:

Australia: Iredale, 1937a, pp. 300–301.

Bismarcks: I. and B. Rensch, 1929, pp. 84–86; I. Rensch, 1937, pp. 602–605.

Solomon Islands: Dell, 1955, p. 425; Solem, in press-A.

Fijis: Mousson, 1870, pp. 180–189.

New Caledonia: Crosse, 1894, pp. 381–383; Hedley, 1898, pp. 102–104; Cockerell, 1930; Franc, 1957, pp. 40–42.

Lord Howe Island: Iredale, 1944, pp. 303–307.

Norfolk Island: Iredale, 1945, pp. 49–50.

Specimens of most of the species were examined (UMMZ and ANSP). It is not possible to recognize phyletic groups, but certain species are very similar in shape.

Thus, the following have a constricted body whorl and flaring aperture:

*P. martensi* H. Adams, 1866: Fiji (UMMZ 87918, ex Walker, Ponsonby, Bednall); Tongatabu, Tonga (UMMZ 87919, ex Walker, Ponsonby, Schlüter), a new locality record.

*P. distorta* Mousson, 1869: Viti Levu, Fiji (ANSP 13235, ex Godefroy); Suva Bay, Viti Levu (UMMZ 88697, ex Walker, Ponsonby).

*Palaina*, new species: Florida, Solomon Islands (UMMZ 181755, ex Kuntz!).

*P. schneideri* I. and B. Rensch, 1929: New Britain.

Three species have a V-shaped spire with shallow sutures and the body whorl not constricted (*Macropalaina*):

*P. pomatiaeformis* Mousson, 1870: Fijis.

*P. gardneri* Dell, 1955: Treasury Island, Solomon Islands.

*P. perroquiniana* Crosse, 1871: New Caledonia (ANSP 64179, ex Fulton; UMMZ 87934, ex Walker, Ponsonby, Beddome).

Three species are cylindrical with shallow sutures (*Cylindropalaina*):

*P. subregularis* Mousson, 1870: Fiji.

*P. mariei* Crosse, 1867: New Caledonia (UMMZ 89912, ex Walker, Tomlin).

*P. montrouzieri* Crosse, 1874: New Caledonia (UMMZ 87922, ex Walker, Wetherby; UMMZ 87923, ex Walker, Ponsonby, Marie); Noumea, New Caledonia (ANSP 13233, ex Dupuy); Bourail, New Caledonia (ANSP 150987, ex Cockerell!).

*P. m. humilior* Cockerell, 1930: Bourail, New Caledonia (ANSP 150986, ex Cockerell, paratypes).

The remaining species from the Bismarcks, Fiji, the Solomons, Lord Howe and the New Hebrides have swollen spires, deep sutures, and slightly constricted body whorls. The Norfolk Island *Palmatina* (Iredale, 1945, pp. 49–50) are characterized by a solute body whorl.

The resemblances noted above may be caused by convergence, but the recognition of these "species groups" is useful if for no other reason than to facilitate identifications.

Specimens of New Hebridean *Palaina* were available only from Espiritu Santo. Two species are here recognized: one with the radial ribs widely spaced on the upper spire and closely spaced on the lower spire; the other with the ribs only slightly less widely spaced on the lower spire and body whorl. The larger, more evenly ribbed species is described as *P. sykesi*; the smaller species with crowded ribs on the body whorl is identified as *P. françoisi* Ancey.

Table XIV.—Size Variation in New Hebridean *Palaina*

|                            | <i>P. sykesi</i>                 |                    | <i>P. françoisi</i> |                   |           |
|----------------------------|----------------------------------|--------------------|---------------------|-------------------|-----------|
|                            | Males                            | Females            | Males               | Females           |           |
| No. of specimens . . . . . | 3                                | 10                 | 48                  | 21                |           |
| Height . . . . .           | Mean                             | 3.58               | 4.22                | 2.35              | 2.89      |
|                            | Range                            | 3.30–3.86          | 4.07–4.45           | 2.10–2.61         | 2.70–3.17 |
|                            | S.D.                             | ....               | 0.12                | 0.13              | 0.10      |
| Diameter . . . . .         | Mean                             | 1.83               | 2.14                | 1.17              | 1.49      |
|                            | Range                            | 1.71–1.93          | 2.01–2.27           | 1.06–1.29         | 1.37–1.59 |
|                            | S.D.                             | ....               | 0.089               | 0.068             | 0.049     |
| H/D . . . . .              | Mean                             | 1.95               | 1.97                | 1.99              | 1.94      |
|                            | Range                            | 1.93–2.00          | 1.83–2.22           | 1.82–2.15         | 1.81–2.06 |
|                            | S.D.                             | ....               | 0.04                | 0.083             | 0.043     |
| Whorls . . . . .           | 6 $\frac{3}{4}$ –6 $\frac{1}{8}$ | 6 $\frac{1}{2}$ –7 | 6–6 $\frac{3}{8}$   | 6–6 $\frac{1}{2}$ |           |

Within each sculptural type, there were two size classes (see Table XIV). No preserved specimens were available, but probably the differences reflect sexual dimorphism. In most land prosobranchs the females are considerably larger than the males (H. B. Baker, 1925b, p. 274). Pending study of the soft parts, I have assumed that the larger shells of each species came from females, the smaller from males.



**Palaina françoisi** Ancey. Plate 27, figs. 3, 4.

*Palaina françoisi* Ancey, 1905, *Nautilus*, 19, (4), pp. 44-45—Espiritu Santo, New Hebrides.

*Range*.—Espiritu Santo.

*Material*.—ML 39 (1 male, 1 female), ML 51 (1 male), ML 78 (2 females), ML 95.

*Remarks*.—The unique example of Ancey's species may be in Brussels, Belgium, but it was not seen or located during this study. All of Ancey's Espiritu Santo shells came from the region in which Kuntz collected. Since the original measurements (height 2.75 mm., diameter 1.5 mm., whorls  $6\frac{1}{2}$ ) fall into the range of variation shown by "female" specimens of the smaller species, *françoisi* has been identified with that population.

Of the extralimital species, *P. françoisi* is most similar to *P. godefroyana* (Mousson) and *P. g. latecosta* (Mousson) from Fiji. The two latter species differ in having deeper sutures, more evenly spaced ribbing, and more rounded whorls.

**Palaina sykesi**, new species. Plate 27, figs. 1, 2.

A species of *Palaina* characterized by its subcylindric shape, shallow sutures, evenly spaced radial ribs, and only slightly constricted body whorl. The only other New Hebridean species, *P. françoisi* Ancey, is smaller and has more closely spaced ribs on the body whorl.

Shell sinistral, subcylindric, sutures well marked but not deeply impressed. Spire increasing regularly in size, distinctly asymmetrical, skewed to the right. Aperture ovate, lip moderately expanded, closely appressed to the penultimate whorl. Umbilicus closed. Apical whorls smooth, spire with widely spaced, slightly protractive ribs, gradually becoming closely spaced on body whorl. Fresh specimens with microscopic spiral lines. Operculum not seen. Holotype, 2.14 mm. in diameter, 4.28 mm. high, with  $6\frac{1}{2}$  whorls. Allotype, diameter 1.84 mm., height 3.56 mm., with  $6\frac{3}{4}$  whorls.

*Type*.—University of Michigan Museum of Zoology no. 186158. Collected from stream drift in the Sarakata River Valley, Espiritu Santo, New Hebrides (ML 95), by Robert E. Kuntz in May and June, 1944.

*Allotype*.—UMMZ 186159. From the same locality as the type.

*Paratypes*.—Specimens from the type locality are UMMZ 186160, BPBM, MCZ, and CNHM 62236.

*Remarks*.—Only drift specimens were available. In size and shape *P. sykesi* resembles some of the Bismarck species (I. and B. Rensch, 1929, pp. 84-86) but differs from them by having a circular aperture,

shallower sutures, a less constricted body whorl, and different micro-sculpture. The Lord Howe Island *Palaina* (Iredale, 1944, pp. 303–307) are more obese and have a more rhomboidal aperture and more crowded ribbing.

*Palaina sykesi* is named for the late Ernest Ruthven Sykes, who published papers on New Hebridean non-marine Mollusca in 1903 and 1904.

## Superfamily RISSOACEA

### Family HYDROBIIDAE

American authors have used the family name Amnicolidae and European authors the name Hydrobiidae. The latter has probable priority (*teste* Morrison) and has been adopted here.<sup>1</sup> Thiele (1928b and 1929, pp. 136–156) and Wenz (1938–44, pp. 555–581) published comprehensive classifications based primarily on radular structure. Recent studies by Berry (1943) and Morrison (1949) have suggested that the verge is an important aid to understanding hydrobiid relationships, but in only a few species have the vergic structures been described.

Following Pilsbry (1948, p. 1065) and Clench and Turner (1948), I have listed the Truncatellidae as a separate family.

One hydrobiid, *Fluviopupa brevior* (Ancey), is found in the New Hebrides. *Fluviopupa* was established by Pilsbry (1911) for a Fijian species, and the genus has been reviewed by Hubendick (1952). In accordance with the classification of Thiele, *Fluviopupa* is here assigned to the subfamily Hydrobiinae, tribe Littoridinae.

### Genus FLUVIOPUPA Pilsbry, 1911

Shell minute, pupiform, with obtuse apex and only slightly rounded whorls. Aperture ovate, vertical or sloping forward below, peristome completely or almost completely free from upper portion of body whorl. Operculum thin, horny, paucispiral, with subcentral nucleus. Radula typically amnicolid, central (4–5)–1–(4–5) / (2–4)–(2–4), lateral with 7–12 cusps, marginals with about 30 minute cusps. Penis with single duct, tip simple or bilobed, some species with a median bulb. (Modified from Pilsbry, 1911, p. 549, and Hubendick, 1952.)

*Type species.*—*Fluviopupa pupoidea* Pilsbry.

<sup>1</sup> Opinion 475 of the International Commission on Zoological Nomenclature (issued July 31, 1957) validates the name Bithynidae of Gray, 1857. Whether or not *Bithynia* (= *Bulimus* Scopoli, 1777) and *Hydrobia* belong to the same family is uncertain. In any case, I prefer to use the more familiar name Hydrobiidae, regardless of the exact relationship of the two genera.

*Remarks.*—Hubendick (1952) summarized previous information on *Fluviopupa*, described two species from Rapa, and indicated a number of probable relatives from the Pacific Ocean. My study of specimens (UMMZ) has enabled me to make several additions to Hubendick's survey.

Iredale (1944, p. 332) proposed names for many *Fluviopupa* from Lord Howe Island and divided them into two genera, *Fluviorissoina* and *Pupidrobia*, without giving illustrations or adequate descriptions. The original study on Lord Howe and Norfolk Island mollusks was done by H. B. Preston, who carefully selected "types" and distributed many new species under manuscript names. Iredale (1944, 1945), working from a series of "cotypes" and the general collection in the Australian Museum (Sydney), published reviews of the Lord Howe and Norfolk fauna. He used most of Preston's manuscript names as his own, but he changed a few names and reported on additional material. Preston's collection was purchased by Bryant Walker and is now in the University of Michigan Museum of Zoology. All of Iredale's species were represented by shells and operculi. No soft parts were available, but *Fluviorissoina* and *Pupidrobia* show no conchological criteria justifying generic separation from *Fluviopupa*.

The New Hebridean *Fluviopupa brevior* is most similar in shell structure to the Fijian *F. pupoidea*, but the latter is larger and more cylindrical, and has a proportionately smaller aperture.

**Fluviopupa brevior** (Ancey). Plate 6, fig. 11; plate 27, figs. 5, 6.

*Potamopyrgus brevior* Ancey, 1905, *Nautilus*, 19, (4), p. 46—Vate Island, New Hebrides.

*Potamopyrgus* sp. J. R. Baker, 1929, *Man and Animals in the New Hebrides*, p. 148—Steaming Hill Lake, Gaua, Banks Group.

*Range.*—Vate, Espiritu Santo, Gaua.

*Material.*—ML 69, ML 78, ML 79, ML 85b, ML 87, ML 95.

*Remarks.*—The location of the unique specimen is unknown to me. Layard mentioned a "*Hydrobia*" from Vate in an invoice of specimens sent to Hartman, but the specimens could not be found in the Carnegie Museum collection. Little would be gained by describing the Espiritu Santo population as a new species, simply because they are from another island, and I have applied the name *brevior* to the entire complex.

I examined about 280 specimens, half of them preserved in alcohol. The variation in a small sample is summarized in Table XV. The males were generally smaller than the females, but the sizes over-

lapped and size alone cannot separate male and female specimens. Destruction of the shell was necessary in order to get at the retracted animal.

Fifteen individuals were dissected. The males were much more heavily pigmented than the females. Mr. Harold J. Walter of the University of Michigan Museum of Zoology informs me (personal communication) that in the North American hydrobiid, *Pomatiopsis*, the female is very dark and the male very light in color.

Table XV.—Size Variation in *Fluviopupa* and *Omphalotropis*

| Lot no.....           |       | <i>F. brevior</i> | <i>O. setocincta</i> | <i>O. poecila</i> | <i>O. conella</i> |
|-----------------------|-------|-------------------|----------------------|-------------------|-------------------|
|                       |       | ML 69             | ML 40                | ML 31d            | CM & UMMZ         |
| No. of specimens..... |       | 27                | 29                   | 79                | 6                 |
| Height.....           | Mean  | 2.08              | 4.81                 | 6.94              | 4.29              |
|                       | Range | 1.71-2.40         | 4.47-5.23            | 5.56-8.55         | 3.87-4.97         |
|                       | S.D.  | 0.14              | 0.20                 | 0.81              | 0.35              |
| Diameter.....         | Mean  | 1.23              | 3.22                 | 5.72              | 3.22              |
|                       | Range | 1.03-1.41         | 2.88-3.65            | 4.70-6.81         | 2.86-3.38         |
|                       | S.D.  | 0.08              | 0.16                 | 0.64              | 0.22              |
| H/D.....              | Mean  | 1.69              | 1.50                 | 1.21              | 1.37              |
|                       | Range | 1.56-1.79         | 1.37-1.59            | 1.10-1.33         | 1.32-1.47         |
|                       | S.D.  | 0.06              | 0.053                | 0.048             | 0.058             |
| Whorls.....           |       | .....             | 5-5½                 | 5¼-6¼             | 5½-6              |

Without destroying the shells, it was impossible to establish sex ratios or the degree of sexual dimorphism. In the field notes, Kuntz records that dicrocoeliid cercariae were recovered from the animals.

*Fluviopupa brevior* was collected alive in quiet fresh-water pools of the Sarakata River on rocks, twigs, and leaves. Both *Physastra layardi* and *Gyraulus montrouzieri* were collected at the same stations. There can be no question but that *Fluviopupa brevior* is a true fresh-water snail and not an estuarine species.

The radula of *F. brevior* did not differ from those figured by Hubendick (1952). The penis, however, showed an important modification (pl. 6, fig. 11). As in the other species, there is a single duct in the verge, but the tip in *brevior* is distinctly bilobate. In this respect, *brevior* more closely resembles the Rapan shells than the Fijian. I saw no significant variation in the shape of the verge in the eight males dissected. In the time available, it was not possible for me to undertake a study of the internal genital anatomy.

## Family TRUNCATELLIDAE

Clench and Turner (1948) reviewed current classification and presented a nomenclatural catalogue of the Truncatellidae. Pilsbry (1948, pp. 1065-68) summarized what little is known of their ecology and method of locomotion.

Truncatellids live in scattered colonies among the debris just above high-water mark. They are thus quite well situated for mechanical dispersal by storms and currents. Most of the numerous named forms will probably be found to be variants of a few widely distributed species.

Quoy and Gaimard (1832-35, p. 186, pl. 12, figs. 27-30) described *Cyclostoma striata* from Vanikoro Island. The specimens were subsequently lost (Clench and Turner, 1948, p. 207), and the original figures and description are unrecognizable. Probably *C. striata* was a truncatellid, but since the types are destroyed and the name unrecognizable, *striata* must be considered a nomen dubium.

The only species definitely known from the New Hebrides is the extremely common, wide-ranging *Truncatella guerinii* A. and J. B. Villa. Cox (1868, p. 48, no. 181) reported a Japanese species, *T. pfeifferi* von Martens, from Erromanga, but the record needs confirmation.

**Truncatella (Truncatella) guerinii** A. and J. B. Villa. Plate 27, fig. 7.

*Truncatella guerinii* A. and J. B. Villa, 1841, Conchy. terr. fluv. Mediolani, p. 59—Reunion.

*Truncatella valida* Pfeiffer, 1856, Zeitschr. f. Malak., 3: 182; Cox, 1868, Exchange List, p. 48, no. 103—Aneiteum; Sykes, 1903, Proc. Malac. Soc. London, 5: 199—Resolution Bay, Tanna (J. J. Walker).

*Truncatella pacifica* Pease, Mabile, 1895, Bull. Soc. d'Hist. Nat. d'Autun, 8: 401—New Hebrides (François).

*Truncatella (Truncatella) guerinii* A. and J. B. Villa, Clench and Turner, 1948, Occ. Pap. Mollusks, 1, (13), pp. 167-169, pl. 23, figs. 12-13.

*Range*.—Aore, Vate, Aneiteum, Tanna, Erromanga(?). Extraliminally from Africa to Japan, New Caledonia, and the Society Islands.

*Material*.—Aore (MCZ 192072, W. L. Nutting); "Woody Island," New Hebrides (ANSP 12617, ex Cox); Vate (DMNZ, W. H. Dawbin!).

*Remarks*.—Colonies of *T. guerinii* will probably be discovered on the shore line of every New Hebridean Island.

Family ASSIMINEIDAE (= **RealIIDae**, **Synceridae** of authors)

There is some confusion as to the correct name to be used for this family. Iredale (1941, p. 59) believed that *Realia* must replace *Omphalotropis*, rather than being used for the New Zealand cyclophorid *Liarea* (see Thiele, 1929, p. 104). If Iredale is correct, then the family name must be RealIIDae Pfeiffer, 1858. Abbott (1949, p. 263) stated that there is no evidence for Iredale's conclusion that Gray's *Figures of Molluscous Animals*, volume 4, appeared before June, 1850. The introduction is dated February 12, 1850, but undoubtedly it appeared several months later. Kobelt (1906, pp. 49, 121, 138) named the subfamilies Garrettinae and Adelomorphinae, both of which have priority over the Assimineidae and Omphalotropidinae of Thiele (1927, pp. 125-127). The systematic position of Kobelt's subfamilies is uncertain and I prefer to utilize Thiele's name. Several authors substituted *Syncera* Gray, 1821, for *Assimineea* Fleming, 1828. Iredale (1922) showed that *Syncera* is a nomen nudum and thus neither *Syncera* nor the Synceridae can replace *Assimineea* or the Assimineidae.

Kobelt (1906), Thiele (1927, 1929, pp. 168-173) and Wenz (1938-44, pp. 631-640) presented synoptic classifications of the Assimineidae. Recently, I. Rensch (1937, pp. 614-625), Cooke and Clench (1943), Kondo (1944), Clench (1946, 1948, 1955), and Abbott (1949, 1958) published papers on some of the Pacific Island species. The New Hebridean species were reviewed by Ancey (1906).

I could come to no conclusions about the distribution and phylogeny within the family. Radular studies show that very similar shells belong to widely divergent genera, few genotypes have had their soft parts examined, and most species have not been adequately described or figured. Most of the species are referable to *Omphalotropis*, but a single shell from Vate Island (DMNZ) is here tentatively referred to *Assimineea nitida* (Pease). *A. nitida* has been widely dispersed throughout most of Polynesia and has even been reported from Java (see van Benthem Jutting, 1956). Its presence in the New Hebrides, if confirmed, may have resulted from accidental introduction by human agency.

## Key to the New Hebridean Assimineidae

1. Shell with prominent spiral ridges; operculum with nearly central nucleus and calcareous granules on outside. . . . . 2  
Shell macroscopically smooth; operculum with acentric nucleus, horny. . . . . 4
2. Diameter more than 4 mm.; umbilicus without keel. . . . . 3  
Diameter less than 4 mm.; umbilicus with a distinct keel.  
*Omphalotropis (Lyrotropis) conella* Sykes

3. Height at six whorls more than 9 mm. . . . . *O. (L.) annatonensis* (Pfeiffer)  
 Height at six whorls less than 8.5 mm. . . . . *O. (L.) poecila* Ancey
4. Umbilicus with a keel. . . . . *O. (Oriella) setocincta* Ancey  
 Umbilicus without a keel. . . . . *Assiminea (A.) nitida* (Pease)

Genus **ASSIMINEA** Fleming, 1828

*Type species.*—*Assiminea grayana* Fleming, 1828.

*Remarks.*—*Syncera* Gray, 1821, is a nomen nudum (see Iredale, 1922, and Thiele, 1929) although Abbott (1949) and van Benthem Jutting (1956) considered it a validly described genus. Subsequently Abbott (1958, pp. 232–233) reconsidered his position and has accepted *Assiminea*.

The shells of *Assiminea* and *Paludinella* are practically inseparable, and only radular studies can determine the generic position of any particular morph. A single shell from Vate Island seems to belong to the complex usually called *Assiminea nitida* (Pease). The exact relationships of the forms grouped under this name remain to be determined (see Abbott, 1949) and the New Hebridean shell is only tentatively referred to the species *nitida*.

**Assiminea (Assiminea) nitida** (Pease)

*Hydrocena nitida* Pease, 1865, Proc. Zool. Soc. London, 1864: 674—Huahine, Society Islands.

*Syncera nitida* (Pease), Abbott, 1949, Occ. Pap. B. P. Bishop Mus., 19, (15), p. 272, fig. 7.

*Syncera nitida* (Pease), van Benthem Jutting, 1956, Treubia, 23, (2), pp. 355–356, fig. 68.

*Range.*—Vate. Reported from Java, Mauritius, Ceylon, China and the Philippines east to the Society Islands by various authors.

*Material.*—At 800 feet elevation in forest, Vate Island (DMNZ, W. H. Dawbin!). Many Polynesian lots (UMMZ and CNHM).

*Remarks.*—As emphasized above, any assimineid identifications based on single shells are apt to be questionable and the exact reference of the Vate population must await an extensive revision of the Pacific "*Assiminea*" and "*Paludinella*."

Genus **OMPHALOTROPIS** Pfeiffer, 1851

*Type species.*—*Cyclostoma aurantiaca* Deshayes, by subsequent designation (Gude, 1921, p. 355).

*Remarks.*—Iredale (1941, p. 59) and Abbott (1949, p. 262) cite *Omphalotropis hieroglyphica* Ferussac as genotype, but the first type

designation is that of Gude, cited above. The typical section of the genus is found on the Mascarene Islands, but none of these species have had their soft parts examined. Thiele (1927, p. 127) recognized several conchological sections from Pacific Islands. Later, Cooke and Clench (1943), Iredale (1944, p. 301) and Clench (1946, 1948, 1955) described new generic units from the Pacific Islands. After examining specimens or illustrations of all the type species, I placed *Omphalotropis setocincta* Ancey in the section *Oriella* Thiele, 1927, and described below a new section, *Lyrotropis*, for the other species.

Only dried specimens of *Omphalotropis setocincta* were available, but many preserved animals of *O. poecila* were in the Kuntz collections. Both species have the pectinate marginal teeth of the Omphalotropidinae. The verge (pl. 6, fig. 12) of *O. poecila* is very similar to that of *O. cookei* Abbott from the Marianas (Abbott, 1949, p. 265, fig. 1e). I did not study further details of the soft parts, since comparative material was lacking.

#### Section **ORIELLA** Thiele, 1927

Shell very small, ovate-conic. Whorls rounded, with deep sutures, body whorl obtusely angled. Umbilicus narrow, with a strong keel. Aperture vertical, oval, angulated above. Lip thickened, columellar and basal margins slightly expanded. Surface macroscopically smooth with a microsculpture of fine pits and spiral lines. (Modified from Wenz, 1938-44, p. 636.)

*Type species*.—*Omphalotropis submaritima* Quadras and Moellendorff.

*Remarks*.—Study of specimens in the University of Michigan Museum of Zoology revealed several very similar "species" which belong to *Oriella*. Not enough material was available to determine whether they are specifically distinct or only one very wide-ranging species. Besides the genotype, *O. submaritima* from the Marianas, *O. granum* Pfeiffer (= *maritima* Montrouzier) from New Caledonia, *O. moussoni* Pease from Fiji, and probably some of the other *Stenotropis* (see Kobelt, 1906, pp. 85-93) are closely related to *O. setocincta* Ancey.

#### **Omphalotropis (Oriella) setocincta** Ancey. Plate 27, figs. 8, 9.

*Omphalotropis setocincta* Ancey, 1890, Le Naturaliste, 1890: 26—Vate (Glisson!).

*Omphalotropis (Eurytropis) setocincta* Ancey, Kobelt, 1906, Jahrb. Nass. Ver. Naturk., 59: 82, 143.

*Range*.—Vate, Espiritu Santo.

*Material*.—ML 24, ML 40, ML 95; Vate Island (UMMZ 74254, ex Walker, Ponsonby, Boettger, Layard, Glisson, type lot specimens).



*Remarks.*—The living specimens of *O. setocincta* were found under debris or in decaying coconuts relatively near the seacoast, but definitely not under “strand line” conditions. The conchologically similar genus *Assimineia* (= *Syncera*) is an inhabitant of brackish water or intertidal areas (see van Benthem Jutting, 1956, p. 349) and *Paludina* lives in fresh water (op. cit., p. 362). The terrestrial habitat of *Omphalotropis* is a definite contrast.

Of the 150 specimens seen, 135 came from ML 40 and were found in decaying coconuts. The animals had been dried, but radulae were extracted and portions of verges examined in softened material. The radula is almost identical to that of *O. poecila* (pl. 6, fig. 13) and the verge is slender near the base and situated mid-dorsally. In the study of softened specimens, I noticed that the shells of males were slenderer and had a proportionately narrower aperture than did those of females (see pl. 27, figs. 8, 9). No attempt was made to sex the vast majority of the dried animals in ML 40; the measurements of a sample of males and females are summarized in Table XV.

As with *Pleuropoma articulata* (Pfeiffer), it is impossible to determine the specific relationships of *Omphalotropis setocincta*. Both *O. setocincta* and *Pleuropoma articulata* have extremely similar species on many Pacific islands. Insufficient material is available, however, to decide whether one wide-ranging or several closely related species are involved.

### LYROTROPIS, new section

Shell small, solid, trochiform. Whorls slightly flattened with moderately deep sutures, body whorl rounded or obtusely angulated. Umbilicus narrow, with or without basal keel. Aperture slightly protractive, circular, with columellar margin flattened. Lip thin, margin slightly expanded in adults. Surface with several to many prominent spiral lirae crossed by retractive radial riblets. Operculum horny, with only slightly acentric nucleus and varying amounts of calcareous granules deposited on the outer surface. Radula with pectinate marginals.

*Type species.*—*Omphalotropis poecila* Ancey.

*Remarks.*—The operculum of *Lyrotropis* is most similar to that of *Rapanella* (Cooke and Clench, 1943, p. 254, fig. 3) but differs in having a surface deposit of calcareous granules as in *Omphalotropis cookei* (Abbott, 1949, p. 265, fig. 1e). The shell form and sculpture of *Lyrotropis* is most similar to *Pseudocyclotus* from the Solomons and Bismarcks, but *Pseudocyclotus* has non-pectinate marginal teeth and a heavily calcified operculum.

None of the Solomon Island (Solem, in press-A), Bismarck (I. Rensch, 1937, pp. 614–625), or New Caledonian (Franc, 1957, pp.

50–52) *Omphalotropis* appear to be closely related to the New Hebridean species. Indeed, *Lyrotropis* is a very “isolated” group and, if I had followed most recent workers on Pacific assimineids, it would have been called a distinct genus.

The three species, *O. annatonensis* (Pfeiffer), *O. poecila* Ancey, and *O. conella* Sykes, were reviewed by Ancey (1906). *O. conella* is quite distinctive, but the relationship between *poecila* and *annatonensis* is uncertain. They differ primarily in size, and the situation may parallel that found in *Gonatoraphe fornicata*, where populations from different islands are quite different in size (see p. 184). Vate Island specimens of *Omphalotropis poecila* are much smaller than Espiritu Santo shells, but juveniles from Espiritu Santo matched the Vate adults. The one specimen of *O. annatonensis* was much larger than any specimen of *poecila* from Espiritu Santo. The status of *poecila* and *annatonensis* can only be settled by population studies and comparisons of their anatomy.

***Omphalotropis* (*Lyrotropis*) *poecila* Ancey.** Plate 6, figs. 12, 13; plate 26, figs. 9, 10.

*Omphalotropis poecila* Ancey, 1890, Le Naturaliste, 1890: 12—Vate (Glisson); Ancey, 1904, Jour. de Conchy., 52, (4), p. 308; Ancey, 1906, Jour. de Conchy., 53, (3), p. 300.

*Omphalotropis varians* Moellendorff, 1897, Nachr. d. Malak. Gesell., 1897: 166–167—Vate (ex Layard); Sykes, 1903, Proc. Malac. Soc. London, 5: 199—Port Vila, Vate (J. J. Walker).

*Omphalotropis annatonensis* Ancey, 1906, Jour. de Conchy., 53, (3), pp. 300–301, fig. 1—Espiritu Santo and Aurora.

*Omphalotropis* (*Eurytropis*) *poecila* Ancey, Kobelt, Jahrb. Nass. Ver. Naturk., 59: 79, 143.

*Omphalotropis* (*Eurytropis*) *varians* Moellendorff, Kobelt, 1906, Jahrb. Nass. Ver. Naturk., 59: 83.

*Range*.—Vate, Maewo, and Espiritu Santo.

*Material*.—ML 26h, ML 31d, ML 44, ML 46, ML 50, ML 51, ML 63, ML 66, ML 86, ML 95; Vate Island (UMMZ 76621, ex Walker, Ponsonby, Boettger, Layard); New Hebrides (CM).

*Remarks*.—The specimens from Vate Island in the University of Michigan Museum of Zoology may be part of the type lot of *O. poecila*. They are much smaller (average diameter 4.35 mm., average height 3.74 mm.) than the adult shells from Espiritu Santo (see Table XV), but juvenile specimens from Espiritu Santo with  $4\frac{7}{8}$  whorls are identical in size, shape, and sculpture. Ancey's variety *santoensis* referred to examples of *O. poecila* in which the white flammulations are missing. Although it could be applied to the larger shells found on Espiritu

Santo, I consider the size difference to be of little taxonomic importance and I have not utilized the name *santoensis*.

Most of the Espiritu Santo shells have whitish color streaks, but in about 30 per cent of the specimens the color markings were absent. The size variation found in 79 adult specimens from ML 31d is summarized in Table XV. The comparatively large standard deviation is probably the result of sexual dimorphism. Lot ML 31d contained only dead shells, but in other lots the shells of males were smaller than those of females.

The radula (pl. 6, fig. 13) and external male genitalia (pl. 6, fig. 12) are typical of the *Omphalotropidinae*. The teeth are shown as isolated objects rather than in their natural positions (see Kondo, 1944, p. 314, fig. 1). The verge of *O. poecila* is quite similar to that of *O. cookei* Abbott (1949, p. 265, fig. 1e) from Saipan in the Marianas, but it is more slender and has less highly developed basal glands. The shell and operculum of *O. cookei* are quite different from those of *O. poecila*.

### ***Omphalotropis (Lyrotropis) conella* Sykes. Plate 11, fig. 5.**

?*Omphalotropis* sp. Sykes, 1903, Proc. Malac. Soc. London, 5: 200—Renee River, Espiritu Santo.

*Omphalotropis conella* Sykes, 1903, loc. cit., fig. 3—Port Vila, Vate Island (J. J. Walker!).

*Omphalotropis conella* Sykes var., Ancey, 1905, Nautilus, 19, (4), p. 45—Espiritu Santo.

*Omphalotropis (Eurytropis) conella* Sykes, Kobelt, 1906, Jahrb. Nass. Ver. Naturk., 59: 62.

*Range*.—Vate and Espiritu Santo.

*Material*.—Vate Island (UMMZ 75540, ex Walker, Ponsonby, Boettger, Layard; CM, ex Hartman, Layard); Renee River, Espiritu Santo (UMMZ 76539, ex Walker, Ponsonby, Sykes). Photograph of the holotype (BM).

*Remarks*.—*O. conella* is easily separated from the other New Hebridean *Omphalotropis* by its small size, prominent umbilical keel, and trochoidal shape. No operculi or preserved specimens were available.

The Vate Island specimens from Layard are probably part of the type lot. The Renee River individual mentioned by Sykes (1903, p. 200) as *Omphalotropis* sp. is now in the University of Michigan Museum of Zoology. It falls within the range of variation shown by the six Vate Island specimens (see Table XV). No specimens of *O. conella* were found by Kuntz.

**Omphalotropis (Lyrotropis) annatonensis** (Pfeiffer). Plate 26, fig. 8.

*Cyclostoma annatonensis* Pfeiffer, 1856, Proc. Zool. Soc. London, 1855: 105—Aneiteum, New Hebrides (MacGillivray!).

*Omphalotropis (Eurytropis) annatonensis* (Pfeiffer), Kobelt, 1906, Jahrb. Nass. Ver. Naturk., 59: 65.

*Range*.—Aneiteum.

*Material*.—Aneiteum (UMMZ 76520, ex Walker, Ponsonby, Boettger, Layard).

*Remarks*.—The single specimen of *O. annatonensis* examined is 10.0 mm. high, 8.3 mm. in diameter, and has  $6\frac{1}{8}$  whorls. The only difference from *O. poecila* is the much larger size. Pending study of further material of both species, I have retained *O. annatonensis* as a distinct species.

## ANALYSIS OF NEW HEBRIDEAN NON-MARINE SNAILS

### Number of Species

The literature contained approximately 135 specific names which had been applied to shells supposedly found in the New Hebrides. Some were misidentifications, others were based on erroneous locality data, and many have been placed in synonymy. In the zoogeographical discussion, I am recognizing 79 species of land snails from the New Hebrides and Santa Cruz Islands (see below, p. 207): 56 are land pulmonates, 17 are land prosobranchs, 3 are fresh-water inhabitants, and 3 are inter-tidal pulmonates. Several names listed in the systematic review (see *Aneitea*, *Partula*, and *Diplomorpha*) are omitted below since they probably do not represent valid species. Their inclusion would give a distorted picture of the relative prominence of the three genera and unduly increase the marked endemism reported below.

No specimens of *Helix vannaelavae* Cox, 1870, and *Charopa perryi* Smith, 1897, were seen, and the identity of these named forms could not be determined. Of the 79 recognized species, 22 are reported for the first time. The 135 specific names are thus reduced to fifty-seven valid species records.

### Inter-Island Distribution

A list of the species known from each island is given in Appendix II. For the 79 recognized species, there are only 152 island records (1.92 records per species).

This lack of locality data prevented any detailed analysis of speciation and distribution within the New Hebrides. Only twenty-five islands have any land snails reported from them; ten islands have more than 3 species; five islands more than 10; and only one island, Espiritu Santo, more than 25. Five islands, Aneiteum, Erromanga, Tanna, Vate, and Espiritu Santo account for 77 per cent (117) of the species records; Aneiteum, Vate, and Espiritu Santo for 63 per cent (95); Vate and Espiritu Santo for 49 per cent (75); and Espiritu Santo alone for 32 per cent (48). Forty-four of the 79 species have been reported from only a single island, but at least 20 of these should be rather widely distributed.

Robert E. Kuntz obtained 41 of the 48 species known from Espiritu Santo; 24 were new records. Three of these were introduced, and the shells of the other 21 were all less than 7 mm. in diameter. Kuntz's most prolific sample was river drift (ML 95). It contained 38 species, 8 of which were found *only* in this sample. Kuntz's collections were limited to southeastern Espiritu Santo (see pls. 1 and 2) and undoubtedly many more species remain to be discovered in the vastly greater unexplored sections of the island. Even Espiritu Santo cannot be considered adequately explored for mollusks.

Practically no mollusks are known from the large islands between Espiritu Santo and Vate (see pl. 1), and, except for Espiritu Santo, no island has more than a few minute snails reported from it. The easiest way for a non-malacologist to collect minute snails is in river drift. Kuntz's one drift sample contained 90 per cent of all the species he found. Drift has the disadvantage of containing only dead shells, but it provides specimens from a variety of habitats and is the only feasible method for an untrained collector to find minute species.

In view of the limited number of locality records, little can be said about distribution patterns within the New Hebrides. Many species range throughout the archipelago. Others are known from only one island but probably are equally widely distributed. There are no clear faunal dissimilarities between the northern and southern islands, and no faunal areas can be recognized. Extensive collecting may change the picture, but I suspect the islands will prove to have a singularly homogeneous fauna. Probably this can be traced to the unstable topography. Relatively long-term maintenance of barriers to dispersal is necessary for successful speciation. A continuing alternation of separation and reunion of populations through geological time would tend more toward variation within species than to separation into species.

Only two of the Santa Cruz Islands, Vanikoro and Santa Cruz, have land snails reported from them. With one exception (*Papuina charlottae* Jaeckel and Schlesch) all the species are closely and obviously related to New Hebridean shells and unrelated to Solomon Island or Fijian taxa. *Papuina charlottae* probably is a mislabeled Solomon Island shell. Only the holotype is known, and the source of the specimen has been responsible for other erroneous localities.

In regard to land snails, the Santa Cruz Islands form a single unit with the New Hebrides. A similar situation apparently exists in insects (Gressitt, 1956, p. 15), although the reptile fauna (p. 312) shows considerable differences. In discussing the land snails, the Santa Cruz and New Hebrides are hereafter referred to jointly as the New Hebrides.

Perhaps the only definite indication of an inter-island distributional pattern can be seen in a parallelism between the snails of the southern New Hebrides and the Santa Cruz Islands. *Trochomorpha bakeri* from Aneiteum is much more similar to the Vanikoro Island *Trochomorpha* sp. than to the central New Hebridean *T. rubens*; the Vate Island *Dendrotrachus e. eva* is represented in the Santa Cruz and Banks Islands by *D. e. stramineus*, with the quite different *D. layardi* on Espiritu Santo; and the southern New Hebridean *Placostylus salomonis* is more closely related to the Santa Cruz *P. hullianus* than to the Espiritu Santo *P. bicolor* (Sykes, 1903, reported *P. salomonis* from Espiritu Santo, but the record needs confirmation).

The data listed above are insufficient to draw anything more than very tentative conclusions, but the immediately suggested idea is that Espiritu Santo has served as a dispersal center from which both the southern New Hebrides and Santa Cruz Islands have been populated. Until the islands have been much more thoroughly explored for land snails, however, this can only be regarded as a tentative suggestion.

### Endemism

On most Pacific Islands it is possible to recognize species having one of five relatively distinct types of distribution: (a) The "tropical tramps" which have been spread throughout the world by commerce of the last 200 years; (b) species widely dispersed over the Pacific by primitive man; (c) species found in only two archipelagos; (d) species endemic to an island or archipelago with congeneric relatives in other regions; and (e) species belonging to a genus found only in one archipelago. Most species can be easily placed in one of the five categories, but a few are of uncertain relationship.

In the following list of the 79 recognized species, the symbols indicate whether the species are endemic (E), found on another island group (N), very widely distributed in the Pacific (W), or a "tropical tramp" (T).

SYSTEMATIC LIST OF NEW HEBRIDEAN AND SANTA CRUZ LAND  
AND FRESH-WATER MOLLUSCA

PULMONATA SYSTELLOMMATOPHORA

Oncidiacea

Oncidiidae

*Oncidium peronii* Cuvier—W

*Oncidium verruculatum* Cuvier—W

*Oncis* aff. *martensi* Plate—W

Soleolifera

Veronicellidae

*Angustipes plebeius* (Fischer)—T

*Eleutherocaulus alte* (Ferussac)—W

PULMONATA STYLOMMATOPHORA

Tracheopulmonata

Athoracophoridae

*Aneitea macdonaldi* Gray—E

*Aneitea speiseri* Grimpe and Hoffmann—E

Heterurethra

Succineidae

*Succinea* (*Papusuccinea*) *kuntziana* Solem—E

Orthurethra

Pupillidae

*Gastrocopta pediculus* (Shuttleworth)—W

Tornatellinidae

*Elasmias apertum* (Pease)—W

*Lamellidea pusilla* (Gould)—W

Enidae

*Rhachistia histrio* (Pfeiffer)—T(?)

Partulidae

*Partula macgillivrayi* Pfeiffer—E

*Partula pyramis* Hartman—E

*Partula auraniata* Hartman—E

*Partula milleri* Solem—E

*Partula vanikorensis* (Quoy and Gaimard)—E

Sigmurethra

Aulacopoda

Arionacea

Endodontidae

*Phrixgnathus glissoni* (Ancey)—E

*Phrixgnathus tenuiscriptus* (Ancey)—E

*Discocharopa planulata* Solem—E

*Mocella euryomphala* Solem—E

*Reticharopa geddiei* Solem—E

*Reticharopa stenopleura* Solem—E

*Reticharopa latecosta* Solem—E

*Reticharopa helwa* (Cox)—E

*Reticharopa* sp.—E

Limacacea

Helicarionidae

Euconulinae

*Wilhelminaia* aff. *mathildae* Preston—W(?)

*Coneuplecta* (*Sitalina*) *microconus* (Mousson)—W

*Coneuplecta* (*Conibycus*) *bicarinata* Solem—E

Microcystinae

*Liardetia* (*Liardetia*) *samoensis* (Mousson)—W

*Diastole subcarinata* Solem—E

*Lamprocystis guttula* (Pfeiffer)—E

*Lamprocystis mendañae* Solem—E

Sesarinae

*Orpiella* (?*Halozonites*) *retardata* (Cox)—E

*Dendrotrochus* (*Santotrochus*) *eva* (Pfeiffer)—E

*Dendrotrochus* (*Santotrochus*) *layardi* (Hartman)—E

Zonitidae

Trochomorphae

*Trochomorpha* (*Hartmanitrochus*) *rubens* Hartman—E

*Trochomorpha* (*Hartmanitrochus*) *bakeri* Solem—E

*Trochomorpha* sp.—E

Holopoda

Subulinidae

*Subulina octona* (Bruguiere)—T

*Opeas pumilum* (Pfeiffer)—T

*Lamellaxis* (*Allopeas*) *gracilis* (Hutton)—T

Bradybaenidae

*Bradybaena similis* (Ferussac)—T

Camaenidae(?)

*Draparnaudia singularis* (Pfeiffer)—N

*Draparnaudia walkeri* Sykes—E

Bulimulidae

*Placostylus hullianus* (Iredale)—E

*Placostylus fuliginus* (Pfeiffer)—E

*Placostylus salomonis* (Pfeiffer)—E

*Placostylus turneri* (Pfeiffer)—E

*Placostylus bicolor* (Hartman)—E

*Diplomorpha* (*Diplomorpha*) *layardi* Ancey—E

*Diplomorpha* (*Diplomorpha*) *coxi* (Pease)—E

*Diplomorpha* (*Diplomorpha*) *delautouri* (Hartman)—E

*Diplomorpha* (*Quiros*) *bernieri* (Hartman)—E

Paryphantidae

*Delos* (*Hebridelos*) *rapida* (Pfeiffer)—E

*Delos* (*Hebridelos*) *gassiesi* (Pfeiffer)—E

*Delos* (*Hebridelos*) *haasi* Solem—E

*Macrocycloides annatonensis* (Pfeiffer)—E

*Ouagapia santoensis* Solem—E

PULMONATA BASOMMATOPHORA

Planorbidae

*Physastra layardi* (Ancey)—W

*Gyraulus montrouzieri* (Gassies)—N



## PROSOBRANCHIA ARCHAEOGASTROPODA

## Helicinidae

- Pleuropoma varians* (Sykes)—E  
*Pleuropoma taeniata* (Quoy and Gaimard)—E  
*Pleuropoma sublaevigata* (Pfeiffer)—E  
*Pleuropoma albescens* (Hartman)—E  
*Pleuropoma rotella* (Sowerby)—E  
*Pleuropoma articulata* (Pfeiffer)—E or W

## PROSOBRANCHIA MESOGASTROPODA

## Cyclophoracea

## Poteriidae

- Gonatoraphe fornicata* (Pfeiffer)—E

## Pupinidae

- Pupina* (*Kanapa*) *brazieri* (Crosse)—E  
*Pupina* (*Kanapa*) *cumingiana* Pfeiffer—E

## Diplommatinidae

- Palaina françoisi* Ancey—E  
*Palaina sykesi* Solem—E

## Rissoacea

## Hydrobiidae

- Fluviopupa brevior* (Ancey)—E

## Truncatellidae

- Truncatella* *Truncatella guerinii* A. and J. Villa—W

## Assimineidae

- Omphalotropis* (*Oriella*) *setocincta* Ancey—E or W  
*Omphalotropis* (*Lyrotropis*) *annatonensis* (Pfeiffer)—E  
*Omphalotropis* (*Lyrotropis*) *poecila* Ancey—E  
*Omphalotropis* (*Lyrotropis*) *conella* Sykes—E  
*Assimineia* (*Assimineia*) *nitida* (Pease)—W

“*Tropical tramps.*”—During the past few centuries commerce has spread many land snails throughout the tropical and warm-temperate regions of the world. These “tropical tramps” or “culture snails” are of uncertain geographic origin but now live in nearly every tropical country. Five New Hebridean pulmonates belong in this category: the veronicellid, *Angustipes plebeius* (Fischer); the three subulinids; and the helcid, *Bradybaena similaris* (Ferussac). Other “tropical tramps” found in Melanesia and Australia, but not yet reported from the New Hebrides, include the subulinids, *Lamellaxis micra* (Orbigny) and *L. mauritianum* (Pfeiffer); the streptaxid, *Gulella* (*Huttonella*) *bicolor* (Hutton); the edible snails, *Helix aspersa* and *Helix pomatia*; and species of the slug genera, *Deroceras*, *Limax*, and *Arion*. *Rhachistia histrio* (Pfeiffer) may belong to this category. *R. histrio* lives in the New Hebrides, New Caledonia and Queensland, and it may be an African species introduced into the Pacific. Without further study, however, its status cannot be precisely determined.

*Atoll fauna.*—The low coral atolls of the Pacific Ocean have a characteristic but limited snail fauna. The species are minute, widely

distributed, and, at least in some cases, carried from island to island by natives (see Cooke, 1926, pp. 2278-2279). Eight New Hebridean species range throughout most of Polynesia, Micronesia and Indonesia: the veronicellid, *Eleutherocaulus alte* (Ferussac); the pupillid, *Gastrocopta pediculus* (Shuttleworth); the tornatellinids, *Elasmias apertum* (Pease) and *Lamellidea pusilla* (Gould); the helicarionids, *Coneuplecta microconus* (Mousson) and *Liardetia samoensis* (Mousson); and the operculates *Truncatella guerinii* (A. and J. Villa) and *Assimineia nitida* (Pease). One other species, the helicarionid, *Wilhelminaia* aff. *mathildae* Preston, probably lives in Indonesia, northern Melanesia, and the Caroline Islands. It is not known from Polynesia and New Caledonia. The three Oncidiidae are very widely dispersed in the Indo-Pacific. In their mode of distribution (by pelagic larvae) the Oncidiidae are marine rather than terrestrial, and they are not discussed further in this study.

Thirteen of the 56 land pulmonates and two of the 17 land prosobranchs are obvious introductions or are so widely distributed that they are of no value in a zoogeographic analysis. Of the remaining 43 pulmonates and 15 prosobranchs, only one (*Draparnaudia singularis* Pfeiffer) is found elsewhere (New Caledonia). The other 57 are endemic.

The three fresh-water species will be considered later.

*Endemic species.*—Some of the endemic species belong to very widely distributed genera—*Succinea*, *Discocharopa*, *Mocella*, *Macrocycloides*, *Ouagapia*, two species of *Palaina*, *Pleuropoma articulata* (Pfeiffer), the five partulids, and *Omphalotropis setocincta* Ancey—which, at the present time, do not seem to be divisible into subgeneric categories. *Diastole*, *Conibycus*, *Orpiella*, the two species of *Lamprocystis*, three *Delos*, and the other five *Pleuropoma* probably belong to endemic sections or subgenera. Until their anatomy has been studied, however, description of subgeneric units is unwarranted.

The two species of *Dendrotrochus*, three *Trochomorpha*, five *Placostylus*, three *Omphalotropis* (*Lyrotropis*), and two *Pupina* definitely belong to endemic sections or subgenera. A few species—the endemic *Draparnaudia*, *Gonatoraphe*, two *Aneitea*, and two *Phrixgnathus*—belong to genera found in only one other archipelago. The remaining nine species—five *Reticharopa* and four *Diplomorpha*—belong to endemic genera.

*Fresh-water snails.*—Two pulmonates, *Physastra layardi* (Ancey) and *Gyraulus montrouzieri* (Gassies), and one prosobranch, *Fluviopupa brevior* (Ancey), comprise the primary fresh-water snail fauna. *Neri-*

*tina* (sens. lat.) and the Thiaridae are at least partially salt-water tolerant and are not included in this study as being fresh-water organisms. *Physastra layardi* is found in New Caledonia and possibly Fiji and Tonga. *Gyraulus montrouzieri* also lives in New Caledonia, but a different *Gyraulus* is found in the Solomons and Fiji (Solem, in press-A). *Fluviopupa brevior* is endemic, with close relatives in the Fijis and Rapa. The reasons for the decreased endemism of the fresh-water snails are discussed below (pp. 258-259).

*Summary.*—Considering just the seventy-three land dwellers, six species (8.2 per cent) are “tropical tramps,” nine (12.3 per cent) are part of the coral atoll fauna, one (1.4 per cent) is found on one other archipelago, and fifty-seven (79.1 per cent) are endemic. Of the endemic species, fourteen (24.6 per cent) belong to genera found on several archipelagoes, thirteen (22.8 per cent) probably belong to endemic subgeneric taxa, fifteen (26.4 per cent) definitely belong to endemic subgeneric units, six (10.5 per cent) belong to genera found on only *one* other archipelago, and nine (15.7 per cent) belong to endemic genera.

I have repeatedly emphasized that the classification of Pacific land snails is poorly understood and that New Hebridean species have been placed in endemic supraspecific taxa only when sufficient evidence of extralimital affinities allowed possible recognition of phyletic lines. Genera of mollusks are not equivalent to genera of vertebrates (see pp. 26-27), and if the smaller genera of Iredale had been utilized here, quite different results would have been obtained. Perhaps thirty-four genera (compared to twenty-five) of which twenty-three were endemic (compared to two) would have been recognized.

### Distribution of New Hebridean Land Snail Taxa

If we exclude the five or six “tropical tramps,” nine atoll species, three onciidiids, *Pleuropoma articulata*,<sup>1</sup> and *Omphalotropis setocincta*,<sup>1</sup> there are fifty-nine species (three living in fresh water) with limited enough distributions to be useful in a zoogeographic analysis. The fifty-six terrestrial species are placed in twenty-four genera, of which only two, *Reticharopa* and *Diplomorpha*, are endemic. The genera belong to fourteen different families.

The distribution of the families and genera with New Hebridean endemic species is shown in Tables XVI and XVII and figures 7 and 8.

<sup>1</sup>These two species may be widely distributed “strand-line” dwellers (see pp. 177, 200).

Table XVI.—Distribution of New Hebridean Families

| Family                             | NG <sup>4</sup> | SI | NH | NC | NZ | F | T | A              | C |
|------------------------------------|-----------------|----|----|----|----|---|---|----------------|---|
| Athoracophoridae.....              | x               | ?  | x  | x  | x  |   |   | x              |   |
| Succineidae <sup>1</sup> .....     | x               | x  | x  | x  | x  |   | x | x              | x |
| Partulidae <sup>1</sup> .....      | x               | x  | x  |    |    | x | x |                | x |
| Endodontidae <sup>1</sup> .....    | x               | x  | x  | x  | x  | x | x | x              | x |
| Helicarionidae <sup>1</sup> .....  | x               | x  | x  |    |    | x | x | x              | x |
| Zonitidae <sup>1</sup> .....       | x               | x  | x  |    |    | x | x | x              | x |
| <i>Draparnaudia</i> .....          |                 |    | x  | x  |    |   |   |                |   |
| Bulimulidae.....                   |                 | x  | x  | x  | x  | x |   | x <sup>2</sup> |   |
| Paryphantidae <sup>1</sup> .....   | x               | x  | x  | x  | x  | x | x | x              | x |
| Camaenidae.....                    | x               | x  |    |    |    |   |   | x              |   |
| Helicinidae <sup>1</sup> .....     | x               | x  | x  | x  |    | x | x | x              | x |
| Cyclophoridae.....                 | x               | x  |    |    | ?  |   |   | x <sup>3</sup> |   |
| Poteriididae <sup>1</sup> .....    |                 |    | x  | x  | ?  | x |   |                | x |
| Pupinidae.....                     | x               | x  | x  |    | ?  | x |   | x              | x |
| Diplommatinidae <sup>1</sup> ..... | x               | x  | x  | x  | x  | x | x | x              | x |
| Assimineidae <sup>1</sup> .....    | x               | x  | x  | x  | x  | x | x | x              | x |

<sup>1</sup> Also in Samoa. <sup>2</sup> A different subfamily. <sup>3</sup> Only in northern Queensland.

<sup>4</sup> NG (New Guinea), SI (Solomon Islands), NH (New Hebrides), NC (New Caledonia), NZ (New Zealand), F (Fiji), T (Tonga), A (Australia), C (Caroline Islands).

Table XVII.—Distribution of New Hebridean Genera

| Genus                                   | NG <sup>4</sup>  | SI  | NH | NC   | NZ  | F   | T   | A              | C    |
|---|------------------|-----|----|------|-----|-----|-----|----------------|------|
| <i>Aneitea</i> .....                    | R <sup>5</sup>   | ?   | x  | x    | R   |     |     | R              |      |
| <i>Papusuccinea</i> <sup>1</sup> .....  | x                | x   | x  | x    | x   |     | x   | R              | R(?) |
| <i>Partula</i> <sup>1</sup> .....       | x <sup>2</sup>   | x   | x  |      |     | x   | x   |                | x    |
| <i>Phrixgnathus</i> .....               |                  |     | x  |      | x   |     |     |                |      |
| <i>Discocharopa</i> .....               | ?                | ?   | x  |      | x   |     |     | x              |      |
| <i>Mocella</i> <sup>1</sup> .....       |                  | x   | x  |      | x   | x   | x   | x <sup>3</sup> | R    |
| <i>Reticharopa</i> .....                | R                | ?   | x  |      |     |     |     |                |      |
| <i>Conibycus</i> .....                  | ?                | ?   | x  |      |     |     |     |                |      |
| <i>Diastole</i> <sup>1</sup> .....      | ?                | ?   | x  |      |     | (x) | (x) |                |      |
| <i>Lamprocystis</i> <sup>1</sup> .....  | (x) <sup>6</sup> | ?   | x  |      |     | (x) | (x) | (x)            |      |
| <i>Orpiella</i> .....                   | (x)              | (x) | x  |      |     | (x) | (x) | (x)            |      |
| <i>Dendrotrochus</i> .....              | ?                | (x) | x  |      |     |     |     |                | (x)  |
| <i>Trochomorpha</i> <sup>1</sup> .....  | (x)              | (x) | x  |      |     | (x) | (x) |                | (x)  |
| <i>Draparnaudia</i> .....               |                  |     | x  | x    |     |     |     |                |      |
| <i>Placostylus</i> .....                |                  | (x) | x  | (x)  | x   | (x) |     |                |      |
| <i>Diplomorpha</i> .....                |                  |     | x  |      |     |     |     |                |      |
| <i>Delos</i> .....                      |                  |     | x  |      | (x) | x   |     | (x)            | x    |
| <i>Macrocycloides</i> .....             | ?                | x   | x  |      |     |     |     |                |      |
| <i>Ouagapia</i> <sup>1</sup> .....      | x                | x   | x  | x    |     | x   | x   |                |      |
| <i>Pteuropoma</i> <sup>1</sup> .....    | (x)              | ?   | x  | x(?) |     | (x) | (x) | (x)            | (x)  |
| <i>Gonatoraphe</i> .....                |                  |     | x  | R    |     | x   |     |                | R    |
| <i>Pupina</i> .....                     | (x)              | (x) | x  |      |     | (x) |     | (x)            | (x)  |
| <i>Palaina</i> .....                    | x                | x   | x  | x    |     | x   | x   | x              | x    |
| <i>Omphalotropis</i> <sup>1</sup> ..... | (x)              | (x) | x  | (x)  |     | (x) | (x) | (x)            | (R)  |

<sup>1</sup> Also Samoa. <sup>2</sup> One record. <sup>3</sup> In southwest Australia only.

<sup>4</sup> See footnote 4 on Table XVI. <sup>5</sup> A related genus.

<sup>6</sup> A different subgenus.

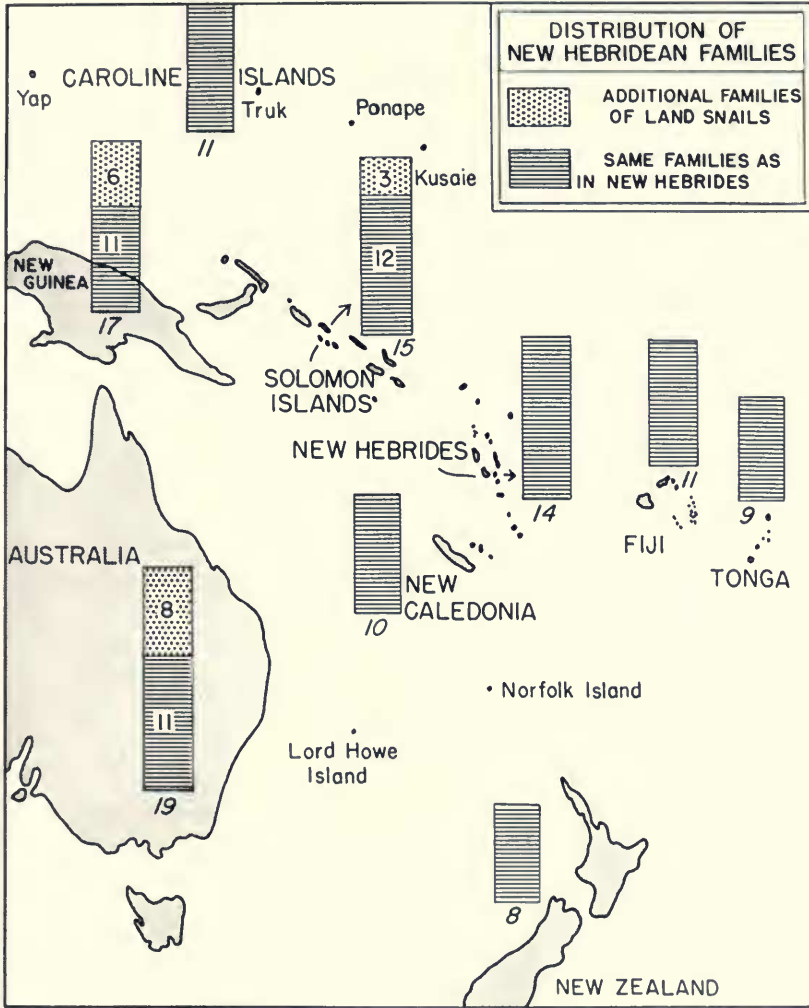


FIG. 7. Distribution of families of New Hebridean land snails.

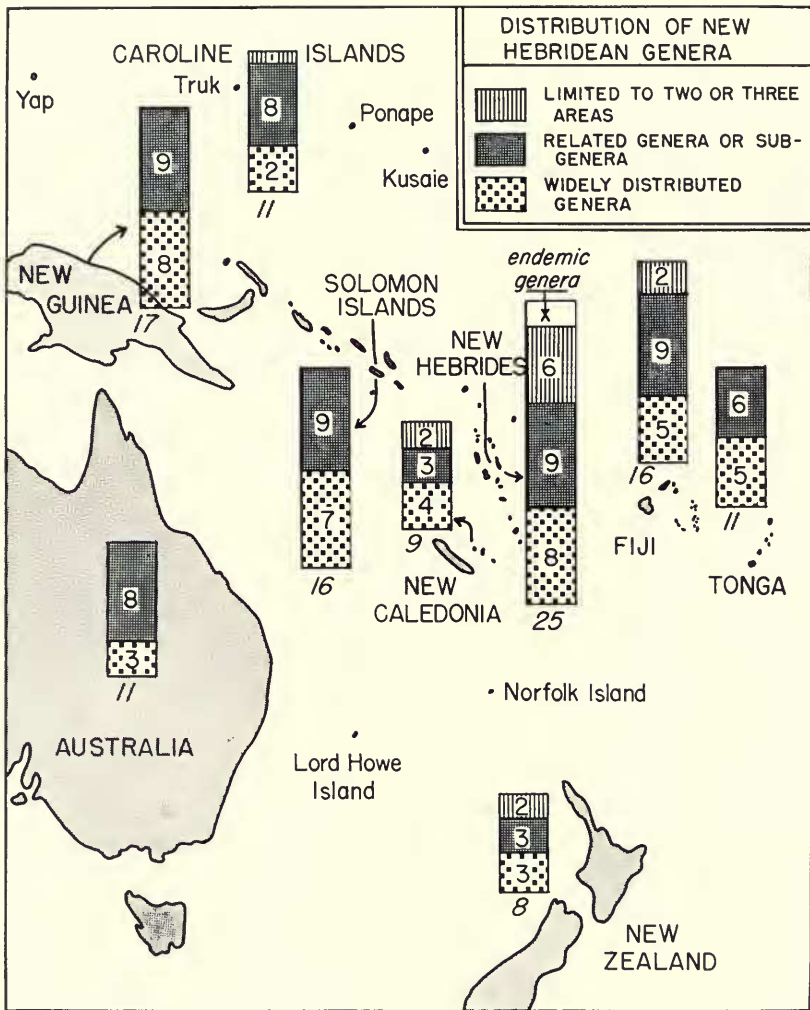


FIG. 8. Distribution of genera of New Hebridean land snails.

The raw data are summarized in figures 7 and 8. New Zealand and Tonga have the fewest New Hebridean families and the Solomons and Fiji the most. New Guinea, the Solomons, and Australia (but none of the other areas) have families which are not found in the New Hebrides. Obviously there are many important faunistic changes, since from two to six of the New Hebridean families are absent from each area.

The New Hebridean genera (fig. 8) show three types of distribution: taxa found in the New Hebrides and only one or two other areas; taxa represented by distinct subgeneric units in other areas; and taxa widely distributed over the Pacific. It proved impossible to include the genera present in these other areas but not in the New Hebrides, and figure 8 shows only the distribution of genera found in the New Hebrides. Because of inadequate collections of small shells, the records for the Solomons and New Guinea are based on a number of probable but unconfirmed records. New Caledonia and New Zealand have the fewest New Hebridean genera, the Solomons, Fiji, and New Guinea the most. The great difference between the New Hebridean and New Caledonian fauna is one of the most striking and most unexpected results of this study. The difference cannot be considered an artifact of collecting, since New Caledonia has been the object of more intensive malacological collecting than any area of the Pacific except Hawaii and the Society Islands. Another important factor is the distribution of genera found on only one or two archipelagos other than the New Hebrides. New Caledonia and Fiji are the nearest islands, but the New Zealand and Caroline Island affinities are surprising, as is the *lack* of any close affinities with the Solomon Islands.

The absolute presence or absence of a taxon is useful, but a more realistic comparison would encompass the *relative importance* of the taxa in each area as well as the general types of distribution shown by the families and genera. Our knowledge about the extent of speciation in land snails over most of the Pacific region is so pitifully inadequate that no comparison of the relative abundance of species in different areas can be attempted. For many areas we have a fair idea of *qualitative*, but very little of *quantitative* content.

## Appendix I: ROBERT E. KUNTZ COLLECTING LOCALITIES ON ESPIRITU SANTO

- ML 1. On dagger plants near Surundo River. Oct., 1943.  
ML 2. Near Turtle River, early morning. Oct. 16, 1943.  
ML 3. Plants and rocks within 20 feet of water. Oct., 1943.  
ML 5. On rocks along shore. Oct. 3, 1943.  
ML 6. Underneath large clam shell, west of Renee River. Oct. 21, 1943.  
ML 7. Turtle Bay. On vegetation, 20-40 feet from stream in deep shade. Oct. 18, 1943.  
ML 8. Decaying coconut. Sarakata River peninsula. Nov., 1943.  
ML 9. On ground in dense jungle, near Sarakata River. Oct., 1943.  
ML 10. On ground in jungle, near Sarakata River. Oct., 1943.  
ML 11. On tree trunk on rainy day. Sarakata River peninsula. Nov. 17, 1943.  
ML 12. On decaying cacao leaves near Malaria Control Headquarters. Oct. 22, 1943.  
ML 13. On decaying cacao leaves near Malaria Control Headquarters.  
ML 14. In decaying coconut, Sarakata River peninsula. Oct., 1943.  
ML 15. Under side of rocks in Renee River. Dec. 30, 1943.  
ML 16. From green leaves and dead wood in damp shaded area. Dec. 28, 1943.  
ML 17. Under side of green leaves of banana-like tree. Dec. 28, 1943.  
ML 18. Dead and decaying sticks and limbs, some from ground. Jan. 6, 1944.  
ML 19. Dead and decaying sticks and limbs; some from ground.  
ML 20. Dead and decaying sticks and limbs; some from ground.  
ML 21. Dead and decaying sticks and limbs; some from ground.  
ML 22-ML 24. Dead limbs on ground near edge of woods. Jan. 13, 1944.  
ML 25. Rocks along shore of Renee River. Occupied by crabs. Dec. 30, 1943.  
ML 26. From vegetation, boards and decaying wood in deep shade in woods. Jan. 20, 1944.  
ML 27. Curtiss Creek, in mud on bottom. Jan. 22, 1944.  
ML 28. Roots of dead trees along bay at mouth of Sarakata River, low tide. Jan. 31, 1944.  
ML 29. Renee River, 1½ miles from mouth, in shallow running water attached to rocks. These eaten by Hawaiians and Filipinos. Dec. 30, 1943.  
ML 30. Same as ML 29, except ½ to 1½ miles upstream.  
ML 31. At edge of jungle during rain. Jan. 22, 1944.  
    a. Under side of decaying logs.  
    b. Tree trunks and fence posts; 1-15 feet up.  
    c. Rotting logs, on trees and ground.  
    d. Trunks of trees and shrubs.  
    e. Leaves of trees and shrubs.  
    f-h. Trunks of trees and shrubs.  
    i. Under sides of boards, rotting logs, coconuts.  
ML 32. Trunks and limbs of trees and shrubs; 1-7 feet up. Feb. 6, 1944.  
ML 33. From alluvial deposits in road cuts, etc. Feb. 6, 1944. Most common within 150 yards of river.  
ML 34. Under logs in Sarakata River valley. Jan. 30, 1944.  
ML 35. Under side of logs in short grass meadow. Jan., 1944.



- ML 36. Along road. Feb. 24, 1944.  
ML 37. From vegetation, trees and shrubs. Feb. 24, 1944.  
ML 38. From lava rocks and coral,  $1\frac{1}{2}$  miles up Renee River; water fresh. Dec. 30, 1943.  
ML 39. Leaves and decaying logs in deep shade. Small snails more abundant under sticks in open places on hillside. Feb. 27, 1944.  
ML 40. In rotting coconuts, Brigstock Point. March 11, 1944.  
a. Under coconut fronds on ground.  
ML 41. Bought on Vao, Malekula, from natives; ready to string. Dec. 5, 1943.  
ML 42. From rocks along and in Renee River,  $1\frac{1}{2}$  miles upstream. Water fresh. Mar. 24, 1944.  
ML 43. Base of papaya tree, Cabar Plantation. Apr. 4, 1944.  
ML 44. From logs and under coconuts. Apr. 13, 1944. Upper Renee River.  
ML 45. Water cress in Cabar Creek. Apr. 15, 1944.  
ML 46. Same as ML 44. On logs.  
ML 47. Under rocks in stream below dam, Brigstock Point. Water swift. April 10, 1944.  
ML 48. Same as ML 47. From stream bottom, some on large rocks.  
ML 49. Venus Island. March 19, 1944. Eaten by natives and Tonkinese.  
ML 52. From water cress, Cabar Creek. Water swift.  
ML 53. From coral rocks in swift-flowing water. Apr., 1944.  
ML 54-57. From coral rocks in swift-flowing water.  
ML 58. From coral rocks in swift-flowing water. Under side of rocks; a few on blades of grass.  
ML 59. Under side of logs. Apr., 1944.  
ML 60. Small semi-permanent pool near Brigstock Point. Chara, lilies and grass in pool. May 5, 1944.  
ML 61-62. Small semi-permanent pool near Brigstock Point. Chara, lilies and grass in pool.  
ML 63. On damp under side of logs in shade near pond. Apr. 25, 1944.  
ML 64. On damp under side of logs in shade near pond.  
ML 65. Semi-permanent pool near Brigstock Point. May 7, 1944. Infected with small stylet cercariae.  
ML 66. From pandanus and other low trees. Apr. 19, 1944.  
ML 67. In swift water below dam, Brigstock Point. Apr. 28, 1944.  
ML 68. Water cress in Cabar Creek. May 25, 1944.  
ML 69. Under side of damp, decaying logs. May 27, 1944.  
ML 70. Shrubs and decaying, fallen trees. Apr., 1944.  
ML 71. From muddy bottom of swift-flowing stream, Naranga Village, 250 feet altitude. May 28, 1944.  
ML 72. On damp ground under trees, buried in decaying logs and under leaves.  
ML 73. From rocks in running water in shade, 2 miles up. June 10, 1944.  
ML 74. On ground among decaying leaves, 300 yards from Renee River. June 8, 1944.  
ML 75. Small stream running into south end of Brigstock Lagoon. From edge of running water in deep shade of mangroves. June 3, 1944.  
ML 76. From ground and dead leaves in shade, 300 yards from Renee River. June 2, 1944.  
ML 77. Cabar Creek. Half buried in muck and decaying vegetation in still places along stream. May 14, 1944.  
ML 78. From rocks in quiet side pool of Sarakata River. Some algae. June 17, 1944.  
ML 79. From rocks and leaves in small pool in Sarakata River bed. Pool shaded, water running slowly. Opisthorcid cercaria. End of logging trail. June, 1944.  
ML 80. In small semi-permanent ground pool in coconut grove, Ratard Plantation. Water muddy. May, 1944.  
ML 81. From rocks on bottom of stream, Renee River. June 19, 1944.

- ML 82. From sticks, dead leaves and duckweed in quiet waters of creek running into Brigstock Lagoon. June 21, 1944.
- ML 83. From decaying leaves and branches, 100 yards from shore line of bay near Renee River. June, 1944.
- ML 84. From stalk and under side of leaves of banana-like plant along Renee River. Found in deep shade where plants are moist all the time. June, 1944.
- ML 85. From quiet pool connected with dammed creek at Brigstock Lagoon. In masses of duckweed, water lilies, and chara. July, 1944.
- ML 86. From leaves of shrubs (a), decaying logs (b) and ground (c) in shaded jungle adjacent to coconut plantation. June 26, 1944.
- ML 87. In small side pool on south bank of Sarakata River. June, 1944. Small snails with dicroclid cercaria.
- ML 88. From shaded large coral rock  $1\frac{1}{2}$  miles up Renee River, in swift water. May, 1944.
- ML 89. From rocks in partly shaded, swift-flowing stream running into Brigstock Lagoon. June, 1944.
- ML 90. From tree trunks in shaded jungle. Aug., 1944.
- ML 91. From shallow trailside pool in well-shaded water protected by overhanging grass near Havet Plantation. July 15, 1944.
- ML 92. Under side of logs and planks off beach near Sarakata River. Aug. 23, 1944.
- ML 93. From small ground pool in coconut grove, Aore Island. Aug. 15, 1944.
- ML 94. Under side of fallen tree trunks on high ground above Brigstock Lagoon. Aug. 24, 1944.
- ML 95. From pile of debris left at base of tree during high water in Sarakata River. May-June, 1944.
- ML 96. Dead shells from banks of stream. July, 1944.

### Marine Collections

- NH 1. Palikulo Bay. Along shore. Oct., 1943.
- NH 2. Woods near shore. Oct., 1943.
- NH 3. Roots of mangrove trees. Oct., 1943.
- NH 4. Near shore at low tide, night. Oct., 1943.
- NH 5. Shore line on Segond Channel. Oct. 20, 1943.
- NH 6. Roots of mangrove trees in Pallikulo Bay. Nov. 22, 1944.
- NH 7. Shores of Segond Channel. Oct. 24, 1943.
- NH 8. Shores of Malo Island. Dec. 14, 1943.
- NH 9. Shores of Palikulo Bay. Nov. 24, 1943.
- NH 10. Segond Channel. Nov. 24, 1943.
- NH 11. Shore of Araki Island, facing sea; steep rough volcanic banks.
- NH 12. Dead tree trunks and rocks along shore at Brigstock Point. Feb. 20, 1944.
- NH 13. Palikulo Bay at low tide.
- NH 14. At night near Brigstock Point. March 20, 1944.
- NH 15. From coral pile. March, 1944.

## Appendix II. MOLLUSCA KNOWN FROM SANTA CRUZ AND NEW HEBRIDEAN ISLANDS

“?”=a doubtful record; \*=literature reference only. Names of questionable validity included. Island sequence from south to north.

### ANEITEUM

|  |   |
|--|---|
| <i>Aneitea macdonaldi</i> Gray             | <i>Draparnaudia s. singularis</i> (Pfeiffer)* |
| <i>Partula macgillivrayi</i> Pfeiffer*     | <i>Draparnaudia s. diminuta</i> Ancey*        |
| <i>Partula eximia</i> Hartman              | <i>Placostylus salomonis</i> (Pfeiffer)       |
| <i>Reticharopa geddiei</i> Solem           | <i>Placostylus fuliginus</i> (Pfeiffer)       |
| <i>Reticharopa helva</i> (Cox)             | ? <i>Diplomorpha coxi</i> (Pease)             |
| <i>Lamprocystis guttula</i> (Pfeiffer)     | <i>Delos haasi</i> Solem                      |
| <i>Coneuplecta microconus</i> (Mousson)    | <i>Macrocycloides annatonensis</i> (Pfeiffer) |
| <i>Liardetia samoensis</i> (Mousson)       | <i>Physastra layardi</i> (Ancey)              |
| <i>Orpiella retardata</i> (Cox)            | <i>Pleuropoma articulata</i> (Pfeiffer)       |
| <i>Trochomorpha bakeri</i> Solem           | <i>Gonatoraphe fornicata</i> (Pfeiffer)       |
| “ <i>Helix</i> ” <i>vannaelavae</i> (Cox)* | <i>Truncatella guerinii</i> A. and J. Villa*  |
| <i>Lamellaris gracilis</i> (Hutton)        | <i>Omphalotropis annatonensis</i> (Pfeiffer)  |

### TANNA

|   |  |
|---|--|
| <i>Aneitea macdonaldi</i> Gray          | <i>Pleuropoma sublaevigata</i> (Pfeiffer)    |
| <i>Succinea kuntziana</i> Solem         | <i>Pleuropoma rotella</i> (Sowerby)*         |
| <i>Rhachistia histrio</i> (Pfeiffer)*   | <i>Pleuropoma articulata</i> (Pfeiffer)*     |
| <i>Partula turneri</i> Pfeiffer         | <i>Pupina cumingiana</i> Pfeiffer            |
| <i>Placostylus salomonis</i> (Pfeiffer) | <i>Truncatella guerinii</i> A. and J. Villa* |
| <i>Physastra layardi</i> (Ancey)        |  |

### FUTUNA

|   |                                  |
|---|----------------------------------|
| <i>Placostylus salomonis</i> (Pfeiffer) | <i>Physastra layardi</i> (Ancey) |
|---|----------------------------------|

### ANIWA

|                                  |
|----------------------------------|
| <i>Physastra layardi</i> (Ancey) |
|----------------------------------|

### ERROMANGA

|   |   |
|---|---|
| <i>Aneitea macdonaldi</i> Gray          | <i>Placostylus turneri</i> (Pfeiffer)*  |
| <i>Partula turneri</i> Pfeiffer         | ? <i>Delos rapida</i> (Pfeiffer)*       |
| ? <i>Partula minor</i> Hartman          | <i>Delos gassiesi</i> (Pfeiffer)        |
| <i>Trochomorpha rubens</i> Hartman      | <i>Pupina brazieri</i> (Crosse)         |
| <i>Liardetia samoensis</i> (Mousson)    | <i>Gonatoraphe fornicata</i> (Pfeiffer) |
| <i>Placostylus salomonis</i> (Pfeiffer) | <i>Truncatella</i> sp.*                 |
| <i>Placostylus fuliginus</i> (Pfeiffer) |   |

## VATE

|   |  |
|---|--|
| <i>Angustipes plebeius</i> (Fischer)*   | <i>Bradybaena similaris</i> (Ferussac)     |
| <i>Eleutherocaulus alte</i> (Ferussac)* | <i>Diplomorpha layardi</i> Ancey           |
| <i>Succinea kuntziana</i> Solem         | <i>Delos rapida</i> (Pfeiffer)             |
| <i>Rhachistia histrio</i> (Pfeiffer)    | <i>Physastra layardi</i> (Ancey)           |
| <i>Partula caledonica</i> (Pfeiffer)    | <i>Pleuropoma sublaevigata</i> (Pfeiffer)  |
| <i>Partula pyramis</i> Hartman          | <i>Pleuropoma articulata</i> (Pfeiffer)    |
| <i>Phrixgnathus glissoni</i> (Ancey)    | <i>Gonatoraphe fornicata</i> (Pfeiffer)    |
| <i>Coneuplecta microconus</i> (Mousson) | <i>Fluviopupa breviar</i> (Ancey)*         |
| <i>Lamprocystis guttula</i> (Pfeiffer)  | <i>Truncatella guerini</i> A. and J. Villa |
| <i>Orpiella retardata</i> (Cox)         | <i>Omphalotropis setocincta</i> Ancey      |
| <i>Dendrotrochus e. eva</i> (Pfeiffer)  | <i>Omphalotropis conella</i> Sykes         |
| <i>Trochomorpha rubens</i> Hartman*     | <i>Omphalotropis poecila</i> Ancey         |
| <i>Opeas pumilum</i> (Pfeiffer)         | <i>Assimineia nitida</i> (Pease)           |
| <i>Subulina octona</i> (Bruguiere)      |  |

## EPI

|  |  |
|--|--|
| <i>Dendrotrochus e. eva</i> (Pfeiffer) | <i>Pleuropoma sublaevigata</i> (Pfeiffer)* |
| <i>Subulina octona</i> (Bruguiere)     |  |

## MALEKULA

|   |                                    |
|---|------------------------------------|
| <i>Phrixgnathus tenuiscripta</i> (Ancey)* | <i>Trochomorpha rubens</i> Hartman |
|---|------------------------------------|

## OMBA

|                                   |                                       |
|-----------------------------------|---------------------------------------|
| ? <i>Diplomorpha peasei</i> (Cox) | <i>Diplomorpha delautouri</i> Hartman |
|-----------------------------------|---------------------------------------|

## MAEWO

?*Omphalotropis poecila* Ancey\*

## ESPIRITU SANTO

|  |  |
|--|--|
| <i>Oncis</i> aff. <i>martensi</i> Plate      | <i>Reticharopa latecosta</i> Solem               |
| <i>Oncidium verruculatum</i> Cuvier          | <i>Reticharopa stenopleura</i> Solem             |
| <i>Angustipes plebeius</i> (Fischer)*        | <i>Reticharopa</i> sp.                           |
| <i>Aneitea maloensis</i>                     | <i>Wilhelminia</i> aff. <i>mathildae</i> Preston |
| Grimpe and Hoffmann*                         | <i>Coneuplecta microconus</i> (Mousson)          |
| <i>Aneitea speiseri</i> Grimpe and Hoffmann* | <i>Coneuplecta bicarinata</i> Solem              |
| <i>Aneitea elisabethae</i>                   | <i>Liardetia samoensis</i> (Mousson)             |
| Grimpe and Hoffmann*                         | <i>Diastole subcarinata</i> Solem                |
| <i>Aneitea r. robsoni</i> Hoffmann*          | <i>Lamprocystis mendañae</i> Solem               |
| <i>Aneitea r. santoensis</i> Solem           | <i>Orpiella retardata depressa</i> Solem         |
| <i>Succinea kuntziana</i> Solem              | <i>Dendrotrochus layardi</i> (Hartman)           |
| <i>Gastrocopta pediculus</i> (Shuttleworth)  | <i>Trochomorpha rubens</i> Hartman               |
| <i>Partula albescens</i> Hartman             | <i>Subulina octona</i> (Bruguiere)               |
| <i>Partula auriana</i> Hartman               | <i>Lamellaxis gracilis</i> (Hutton)              |
| <i>Partula fraterna</i> Hartman              | <i>Opeas pumilum</i> (Pfeiffer)                  |
| <i>Partula carnicolor</i> Hartman            | <i>Bradybaena similaris</i> (Ferussac)           |
| <i>Partula milleri</i> Solem                 | <i>Draparnaudia walkeri</i> Sykes                |
| <i>Phrixgnathus glissoni</i> (Ancey)         | <i>Placostylus bicolor</i> (Hartman)             |
| <i>Phrixgnathus tenuiscriptus</i> (Ancey)    | <i>Placostylus salomonis</i> (Pfeiffer)*         |
| <i>Discocharopa planulata</i> Solem          | <i>Diplomorpha brazieri</i> Hartman              |
| <i>Mocella euryomphala</i> Solem             | <i>Diplomorpha delautouri</i> Hartman            |

ESPIRITU SANTO—*continued*

|   |  |
|---|--|
| <i>Diplomorpha bernieri</i> (Hartman)     | <i>Palaina françoisi</i> Ancey               |
| <i>Ouagapia santoensis</i> Solem          | <i>Palaina sykesi</i> Solem                  |
| <i>Physastra layardi</i> (Ancey)          | <i>Fluviopupa brevior</i> (Ancey)            |
| <i>Gyraulus montrouzieri</i> (Gassies)    | <i>Truncatella guerinii</i> A. and J. Villa* |
| <i>Pleuropoma albescens</i> (Hartman)     | <i>Omphalotropis setocincta</i> Ancey        |
| <i>Pleuropoma sublaevigata</i> (Pfeiffer) | <i>Omphalotropis poecila</i> Ancey           |
| <i>Gonatoraphe fornicata</i> (Pfeiffer)   | <i>Omphalotropis conella</i> Sykes           |
| <i>Pupina brazieri</i> Crosse             |  |

## GAUA, BANKS

|  |                                   |
|--|-----------------------------------|
| <i>Partula fraterna</i> Hartman*           | <i>Physastra layardi</i> (Ancey)* |
| <i>Pleuropoma sublaevigata</i> (Pfeiffer)* | <i>Fluviopupa brevior</i> (Ancey) |

## VANUA LAVA, BANKS

|  |  |
|--|--|
| <i>Partula proxima</i> Hartman*          | <i>Dendrotrochus eva stramineus</i> Sykes* |
| <i>Partula fraterna</i> Hartman*         | ? <i>Trochomorpha rubens</i> Hartman*      |
| <i>Coneuplecta microconus</i> (Mousson)* | <i>Pleuropoma sublaevigata</i> (Pfeiffer)* |

## VALUA, BANKS

|                                  |  |
|----------------------------------|--|
| <i>Succinea kuntziana</i> Solem* | <i>Pleuropoma sublaevigata</i> (Pfeiffer)* |
|----------------------------------|--|

## MOTA ISLAND, BANKS

"*Charopa*" *perryi* Smith\*

## LO ISLAND, TORRES

|  |  |
|--|--|
| <i>Partula auraniiana</i> Hartman*         | <i>Pleuropoma sublaevigata</i> (Pfeiffer)* |
| <i>Dendrotrochus eva stramineus</i> Sykes* |  |

## BUKA-BUKA ISLAND, TORRES

*Partula auraniiana* Hartman\*

## HIU ISLAND, TORRES

|                                   |  |
|-----------------------------------|--|
| <i>Partula auraniiana</i> Hartman | <i>Pleuropoma sublaevigata</i> (Pfeiffer)* |
|-----------------------------------|--|

## "NEW HEBRIDES"

|   |                          |
|---|--------------------------|
| <i>Triboniophorus graeffei</i> Humbert* | <i>Delos haasi</i> Solem |
| <i>Partula radiosa</i> (Pfeiffer)*      |                          |

## VANIKORO, SANTA CRUZ

|  |  |
|--|--|
| <i>Partula vanikorensis</i> (Quoy and Gaimard) | <i>Pleuropoma taeniata</i>                     |
| <i>Trochomorpha</i> sp.*                       | (Quoy and Gaimard)*                            |
|  | <i>Truncatella striata</i> (Quoy and Gaimard)* |

## SANTA CRUZ ISLAND, SANTA CRUZ

|   |  |
|---|--|
| <i>Oncidium peronii</i> Cuvier*           | <i>Placostylus hullianus</i> (Iredale) |
| <i>Dendrotrochus eva stramineus</i> Sykes | <i>Pleuropoma varians</i> (Sykes)      |
| ? <i>Papuina charlottae</i>               |  |
| Jaeckel and Schlesch*                     |  |

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